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CRANIAL STRUCTURE OF †*CHONDROSTEUS ACIPENSEROIDES* RE-EXAMINED: IMPLICATIONS FOR UPPER JAW HOMOLOGIES IN ACIPENSERIFORM FISHES

BY

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Abstract — The Early Jurassic family †Chondrosteidae is considered the sister lineage to all remaining acipenseriforms, the actinopterygian group that includes sturgeons, paddlefishes, and their immediate extinct relatives. As the best-known and oldest †chondrosteid, the Hettangian–Sinemurian †*Chondrosteus acipenseroides* plays a central role in understanding plesiomorphic acipenseriform conditions. Here we present a micro-computed tomographic examination of the cranial anatomy of †*Chondrosteus* based on a laterally compressed skull. We corroborate many aspects of the most recent account of this genus but find additional upper jaw bones not previously reported. These newly recognized ossifications, some dermal and some endoskeletal in origin, bear on hypothesized homologies of upper jaw components in acipenseriforms. First, †*Chondrosteus* possesses a series of up to three toothed dermal bones associated with the ventral margin of the palate. These bones correspond to the dermopalatines of other actinopterygians. We therefore reject identification of the marginal, strap-like bone of the acipenseriform upper jaw as a dermopalatine and accept the historical interpretation of that ossification as a maxilla. Second, two endoskeletal bones are associated with the aboral surface of the palate. The largest of these is a thin sheet matching the bone conventionally interpreted as an autopalatine in other acipenseriforms. It is joined by a smaller, more robust bone that lies at the anterior margin of the jaw and resembles the autopalatine of more generalized early actinopterygians, leading us to suggest the acipenseriform "autopalatine" is in fact the metapterygoid. These new observations support recently revised interpretations of homology based on living species. We conclude by reviewing past candidates for deeper members of the acipenseriform stem than †chondrosteids, including †saurichthyiforms, †*Birgeria*, †*Errolichthys*, †coccolepidids, †*Eochondrosteus*, and a handful of Paleozoic taxa. At present, we find no compelling evidence for an affinity between any of these and acipenseriforms. Paleontological and molecular data indicate that the long, barren acipenseriform stem spans the late Paleozoic and early Mesozoic; identification of its members poses an outstanding challenge in actinopterygian paleontology.

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“The importance of †*Chondrosteus* lies in its probable basal position within Acipenseriformes and the effect that this may have on prescribing plesiomorphic conditions and polarity of character changes within acipenseriforms.”

Hilton and Forey (2009: 428)

“The issue [of acipenseriform jaw evolution] is, however, challenging since the most basal Mesozoic representatives of the group display the same general . . . pattern as found in extant sturgeons . . . The total lack of intermediates makes the transition from the presumed ancestral palaeoniscoid pattern to the condition found in acipenseriforms completely unclear.”

Tsessarsky (2024: 43)

INTRODUCTION

The Early Jurassic †*Chondrosteus acipenseroides* has occupied a central position in debates on acipenseriform systematics and evolution for over 180 years. †*Chondrosteus* is represented by numerous specimens principally from the Hettangian–Sinemurian Blue Lias Formation in the vicinity of Lyme Regis, Dorset, U.K. (for a review of localities, see Hilton and Forey, 2009: 431–432). It was first reported by Agassiz in 1844 as a name only, based on a partial but notably *Acipenser*-like caudal fin reflected by an evocative—but not yet valid—binomial (Agassiz, 1833–1843 [1844]; dates for individual portions provided by Brown in Woodward and Sherborn, 1890: xxv–xxix). Egerton (1858) formally erected the taxon more than a decade later while describing more complete material belonging to several individuals. His contribution made concrete the previously implicit association between †*Chondrosteus* and sturgeons, a view amplified by several authors in the final decades of the 19th century (Davis, 1887; Traquair, 1887; Browne, 1889; Woodward, 1889, 1895) with minimal dissent (Young, 1866). Of these supporting accounts, Woodward’s (1889) overview of sturgeon paleontology proved particularly enduring. His whole-body restoration (Woodward, 1895: fig. 2) appeared in several generations of influential vertebrate paleontology textbooks (Woodward, 1895: fig. 68; Romer, 1933, 1945: fig. 71; Romer, 1966: fig. 78; Carroll, 1989: fig. 6-19b), cementing †*Chondrosteus* as the archetypal early relative of acipenseriforms in general and sturgeons in particular.

Apart from a brief description and illustration of two specimens by Watson (1925: fig. 7; 1928: fig. 15) accompanied by a revised cranial reconstruction (Watson, 1925: fig. 8) later modified by Gardiner and Schaeffer (1989: fig. 21a), essentially no new information on the anatomy of †*Chondrosteus* was presented between the late 1800s and the detailed redescription by Hilton and Forey (2009) over a century later. This most recent examination enriched past accounts, helping to clarify several aspects of cranial anatomy. Importantly, it corroborated the systematic interpretation of Grande and Bemis (1996) and Bemis et al. (1997) that placed †*Chondrosteus* and, by extension, other †chondrosteids as the sister lineage of all remaining acipenseriforms. This stands in contrast to the once-dominant view that †*Chondrosteus* was an immediate relative of sturgeons to the exclusion of paddlefishes, a hypothesis proposed by early workers and which persisted into the cladistic era (Schaeffer, 1973; Patterson, 1982a). This deep position within acipenseriform phylogeny makes †chondrosteids essential for understanding character evolution within this broader group, as well as its divergence from other lineages of ray-finned fishes. †*Chondrosteus* is the oldest and best-known †chondrosteid, represented by numerous fossil specimens. With the younger Toarcian taxa †*Gyrosteus* and †*Strongylosteus* generally receiving little attention (Woodward, 1889; Hennig, 1925; Jaekel, 1929, Cooper et al., 2025), †*Chondrosteus* serves as the representative †chondrosteid and thus the de facto model of a “primitive” acipenseriform.

Despite the substantial advance their re-study of †*Chondrosteus* represented, Hilton and Forey (2009) recognized the limitations of available specimens, nearly all of “which were collected and prepared (such as they were) over 150 years ago” (2009: 433). Breakage and disarticulation due to taphonomic processes coupled with rudimentary preparation means that many aspects of cranial anatomy in †*Chondrosteus* are imprecisely resolved. Although not widely applied to actinopterygian fossils at the time of Hilton and Forey’s (2009) revision, micro-computed tomography (µCT) has subsequently shown considerable value in extracting additional anatomical information from specimens pushed to their limits in terms of external examination (Giles et al., 2017; Argyriou et al., 2022; Giles et al., 2023). Unfortunately, most material of †*Chondrosteus* is not amenable to µCT due to large sizes, mounting in bulky plaster and thick wooden frames, or both. This motivated us to locate material that would be suitable for this kind of imaging, leading to NHMUK PV P 75108 (Fig. 1). Examined externally by Hilton and Forey (2009; where it appears under its earlier catalog number of BMNH P.4341), this specimen comprises the head of a single individual preserved in right lateral view within a free block of matrix small enough to yield good results using lab-based µCT instruments.

Here we describe the anatomy of this specimen of †*Chondrosteus* with the broad goal of filling gaps in past accounts limited by the nature of coarsely prepared historical specimens. We specifically aim to add new paleontological information bearing on the so-called “maxilla-dermopalatine controversy” (Tessarsky, 2024: 57) concerning the identity of the strap-like dermal bone constituting the lateral edge of the upper jaw in living and extinct acipenseriforms (Datovo and Rizzato, 2018). This ossification was historically considered a maxilla (e.g., Grande and Bemis, 1991) but later reinterpreted as a dermopalatine by Findeis (1993) due, in part, to its intimate connection with the palate in the shovelnose sturgeon *Scaphirhynchus platorynchus*. The dermopalatine hypothesis has since gained substantial traction, appearing in most subsequent anatomical accounts of extant (Hilton, 2005; Hilton et al., 2011, 2016, 2020; Warth et al., 2017, 2018) and extinct (Grande and Bemis, 1996; Grande et al., 2002; Grande and Hilton, 2006; Sato et al., 2018; Hilton et al., 2021,

FIGURE 1 — †*Chondrosteus acipenseroides*, photograph of entire specimen consisting of partial skull and shoulder girdle preserved in right lateral view (NHMUK PV P 75108). Abbreviation: *fr*, frontal. White arrow indicates black ink ring, which appears to have been added to indicate the position of the eye.

2023; Hilton and Grande, 2023) acipenseriforms, including †*Chondrosteus* (Hilton and Forey, 2009). However, others have questioned this identification, arguing for reinstatement of the classic interpretation as a maxilla based on structural, topological, and developmental grounds (Datovo and Rizzato, 2018; Tsessarsky, 2024). Doubts have also recently been raised about the identity of the plate-like endoskeletal ossification, long regarded as an autopalatine, apparent in the upper jaw of some acipenseriforms (Tsessarsky, 2024). New details from †*Chondrosteus*, the oldest definitive acipenseriform and member of the sister lineage to all remaining examples of the group, could be especially relevant additions to these debates.

It is our distinct pleasure to provide this contribution in honor of the career and contributions of Lance Grande. Through painstaking work over several decades, Lance has substantially advanced our understanding of acipenseriform anatomy, systematics, and evolution (see Hilton et al., 2025). His polyodontid monograph co-authored with Willy Bemis (Grande and Bemis, 1991) established a new standard for comparative osteological studies of fossil and Recent fishes, followed not long thereafter by a systematic revision of Acipenseriformes that remains the essential morphological survey of higher-level interrelationships within the group (Grande and Bemis, 1996). These foundational contributions are joined by a host of additional acipenseriform studies led by Lance or completed in collaboration with his colleagues and mentees: monumental anatomical treatments of living species (*Acipenser*: Hilton et al., 2011), exquisite descriptions of fossil material (†*Protopsephurus*: Grande et al., 2002; †*Yanosteus*: Hilton et al., 2021) leading to the naming of several new taxa (†*Priscosturion longipinnis*: Grande and Hilton, 2006, 2009; †*Acipenser anisinferos* and †*A. praeparatorum*: Hilton and Grande, 2023; †*Parapsephurus willybemisi* and †*Pugiopsephurus inundatus*: Hilton et al., 2023), critical reviews of extinct and extant acipenseriforms (Bemis et al., 1997; Hilton and Grande, 2006; Schultze et al., 2021), accounts of possible extinct relatives of acipenseriforms (Hilton et al., 2004), and investigation of development in *Polyodon* (Bemis and Grande, 1992, 1999). Examination of previously hidden character states revealed through meticulous mechanical (Grande and Hilton, 2006) or chemical (Grande, 2010) preparation of fossil specimens represents a consistent feature of Lance's work. It is in this vein that we present our virtual preparation of †*Chondrosteus*.

INSTITUTIONAL ABBREVIATIONS AND DAGGER SYMBOL

NHMUK —	The Natural History Museum, London, U.K.
UMMP —	University of Michigan Museum of Paleontology, Ann Arbor, MI, U.S.A.

Our contribution considers both extant and extinct taxa. For clarity, we apply the dagger symbol or obelus ("†") before the names of extinct taxa throughout. This follows the convention used widely in Lance's contributions on fossil and living fishes and was established by two of his mentors, Donn Rosen and Colin Patterson (Rosen and Patterson, 1977; Hilton et al., 2025).

COMPARATIVE MATERIALS

NHMUK PV P 75108 (previously cataloged as BMNH P.4341), a modestly sized specimen preserving the skull and dermal shoulder girdle in right lateral view, represents our principal focus. It is part of the Enniskillen Collection, and thus part of the historic core of the NHMUK fossil fish collection. Like most specimens of †*Chondrosteus*, NHMUK PV P 75108 was collected at Lyme Regis, Dorset, U.K.

Most fossil and living acipenseriforms are well-described, permitting extensive literature-based comparisons. For †Peipiaosteidae, we considered †*Peipiaosteus* and †*Yanosteus* in our comparisons (Grande and Bemis, 1996; Jin, 1999; Hilton et al., 2021). These represent the best-known examples of the two †peipiaosteid subfamilies: †Stichopterinae and †Sphaerosteinae. Putative members of †Chondrosteidae other than †*Chondrosteus* itself require re-examination (Hilton and Forey, 2009), and we have not made extensive comparisons with them here. †*Gyrosteus* is represented mostly by disarticulated bones, while exceptionally preserved articulated skeletons of †*Strongylosteus* were last studied a century ago (Henning, 1925). We follow the convention in the literature that these three genera form a clade but reiterate the sparse evidence for †chondrosteid monophyly indicated by past workers (Grande and Bemis, 1996; Jin, 1999; Cooper et al., 2025).

We addressed a gap in the literature with examination of the type specimen of †*Palaeopsephurus wilsoni* (UMMP VP 22206). This individual was described in detail by MacAlpin (1947) and revisited by Grande and Bemis (1991). Grande and Bemis (1991: 91) noted that the portion of the type containing the jaws was lost several decades prior, leading them to base their re-description on photographs taken from MacAlpin's dissertation (MacAlpin, 1941). The jaws were relocated in the collections of the University of Michigan Museum of Paleontology sometime before 2016. We examined them using µCT to determine the condition of palatal dentition, which is present in some polyodontids (Grande and Bemis, 1991).

METHODS

Computed Tomography

We used a Nikon XT H 225 ST industrial scanner at the CTEES facility, Department of Earth and Environmental Sciences, University of Michigan for imaging fossil material. We made a single scan of †*Chondrosteus acipenseroides*

TABLE 1 — Data availability for taxa sampled in this study.

Specimen	Media type and DOI
†*Chondrosteus acipenseroides*	Tomogram stack (.TIFF)
NHMUK PV P 75108	https://doi.org/10.7302/gj4d-zx58
	Materialise Mimics file (.MCS; 3D surface files (.PLY)
	https://doi.org/10.7302/gqvx-r153
†*Palaeopsephurus wilsoni*	Tomogram stack (.TIFF)
UMMP VP 22206	https://doi.org/10.7302/f1e5-an63

NHMUK PV P 75108 that included most of the block in the field of view (voltage, 150 kV; current, 257 µA; exposure, 4 s; projections, 3141; frames per projection, 2; filter, 2.7 mm copper; effective voxel size, 57.06 µm; option for minimizing ring artefacts was selected). Our scan of †*Palaeopsephurus wilsoni* UMMP VP 22206 was limited to the small block containing the articulated jaws (Grande and Bemis, 1991: fig. 69; voltage, 180 kV; current, 185 µA; exposure, 708 ms; projections, 3141; frames per projection, 1; filter, 0.35 mm copper; effective voxel size, 34.11 µm; option for minimizing ring artefacts was selected). Table 1 summarizes availability of tomographic data and derivatives.

Data segmentation and rendering

Tomographic data for †*Chondrosteus acipenseroides* NHMUK PV P 75108 were segmented using Materalise Mimics v.25 (Materialise Software, Leuven, Belgium; https://www.materialise.com/en/healthcare/mimics-innovation-suite/mimics), with renders for illustrations made in Blender v.2.79 (Blender Project; https://www.blender.org/).

Photogrammetry

A photogrammetric model of †*Chondrosteus acipenseroides* NHMUK PV P 75108 was created using standard protocols for the University of Michigan Online Repository of Fossils (UMORF; https://umorf.ummp.lsa.umich.edu/wp/about/project-methods/). The model is available at https://umorf.ummp.lsa.umich.edu/wp/specimen-data/?Model_ID=1944.

ANATOMICAL DESCRIPTION

NHMUK PV P 75108 (Fig. 1) measures approximately 114 mm from the anterior tip of the jaws to the broken rear margin of the subopercle. With an estimated total length of a little less than a meter based on proportions in published reconstructions (Woodward, 1889), it represents a modestly sized example of †*Chondrosteus*. The specimen is preserved laterally compressed with the right side of the head exposed, in contrast to the more typical dorsoventral flattening seen in other individuals (Hilton and Forey, 2009). Most of the skull is present (Figs. 2–3), including (anatomical terms applied by Hilton and Forey, 2009 in parentheses; see Discussion): approximately nine rostral canal bones of the snout; the lacrimal, jugal, scleral ossicle, and other fragments belonging to the cheek and circumorbital series; the parasphenoid and indeterminate endoskeletal ossifications of the neurocranium; the subopercle and branchiostegals of the operculogular series; the entopterygoid (palatopterygoid), ectopterygoid, dermopalatines, metapterygoid (autopalatine), autopalatine, maxilla (dermopalatine), and incomplete quadratojugal of the upper jaw; the dentary and prearticular of the lower jaw; the hyomandibula, anterior certohyal, and hypohyal of the hyoid arch; the epibranchials and ceratobranchials of the gill skeleton; and the supracleithrum, cleithrum, probable clavicle of the pectoral girdle. Components that are missing entirely include the very tip of the snout and most of the skull roof, with only the dermosphenotic, dermopterotic, and fragment of frontal preserved, all on the right side.

Rostrum and skull roof

Preserved components of the snout are limited to a series of disarticulated and displaced mineralized tubes carrying sensory canals (rcb, Fig. 3). These bear regularly spaced, laterally directed tubules with openings into the main canal.

Only the disarticulated right dermosphenotic and demopterotic of the skull roof are within the field of view of our scan; a portion of the right frontal is also present in the specimen externally (fr, Fig. 1) but not captured in tomograms. The rectangular dermopterotic (dpt, Figs. 2–3) bears a lateral projection and is covered by rugose ornamentation along the lateral margin of its outer surface. A thin, unornamented strip traces the posterior margin, representing overlap for extrascapulars that are not preserved in this specimen (but see Hilton and Forey, 2009: fig. 14). The supratemporal sensory canal branches near the center of the dermopterotic (stcn, Fig. 4). The medial branch continues as the supraorbital canal and exits the anterior margin of the dermopterotic (sobcn, Fig. 4). The lateral branch, representing the infraorbital canal (iocn, Fig. 4), exits from the anterior end of the dermopterotic to extend onto the dermosphenotic. Few actinopterygians show a junction of the supraorbital and infraorbital canals so centrally within the dermopterotic (see images in Gardiner and Schaeffer, 1989), but this feature is common among acipenseriforms (Grande and Bemis, 1991; Hilton et al., 2011).

The dermosphenotic (dsp, Figs 2–3) is flat, rectangular, and defines the posterodorsal corner of the orbit. Its ventral and anterior limbs are barely developed. A ridge on the inner surface of the dermosphenotic marks the path of the sensory canal, which is joined by a complex network of internal sensory canal tubes and tubules that connect to the surface via small pores. The main body of the canal extends longitudinally on the dermosphenotic, turning ventrally to exit the bone (Fig. 4). A small anterior branch is present at this bend in the main canal.

Cheek and Scleral Ossicle

The jugal (jug, Fig. 2) is essentially complete and frames the posterior and much of the ventral edge of the orbit. A crack extends across the upper part of the jugal, separating the main body of the bone from a boot-shaped ossification tightly linked to—but clearly distinct from—the dermosphenotic. It seems likely this fragment is the upper tip of the jugal, as Hilton and Forey (2009: 437) indicate it contacts the dermosphenotic directly with no intervening bones. However, Watson's reconstruction (1925: fig. 8) reported a separate "postfrontal" in this position, identified as an infraorbital in subsequent versions by other authors (Gardiner and Schaeffer,

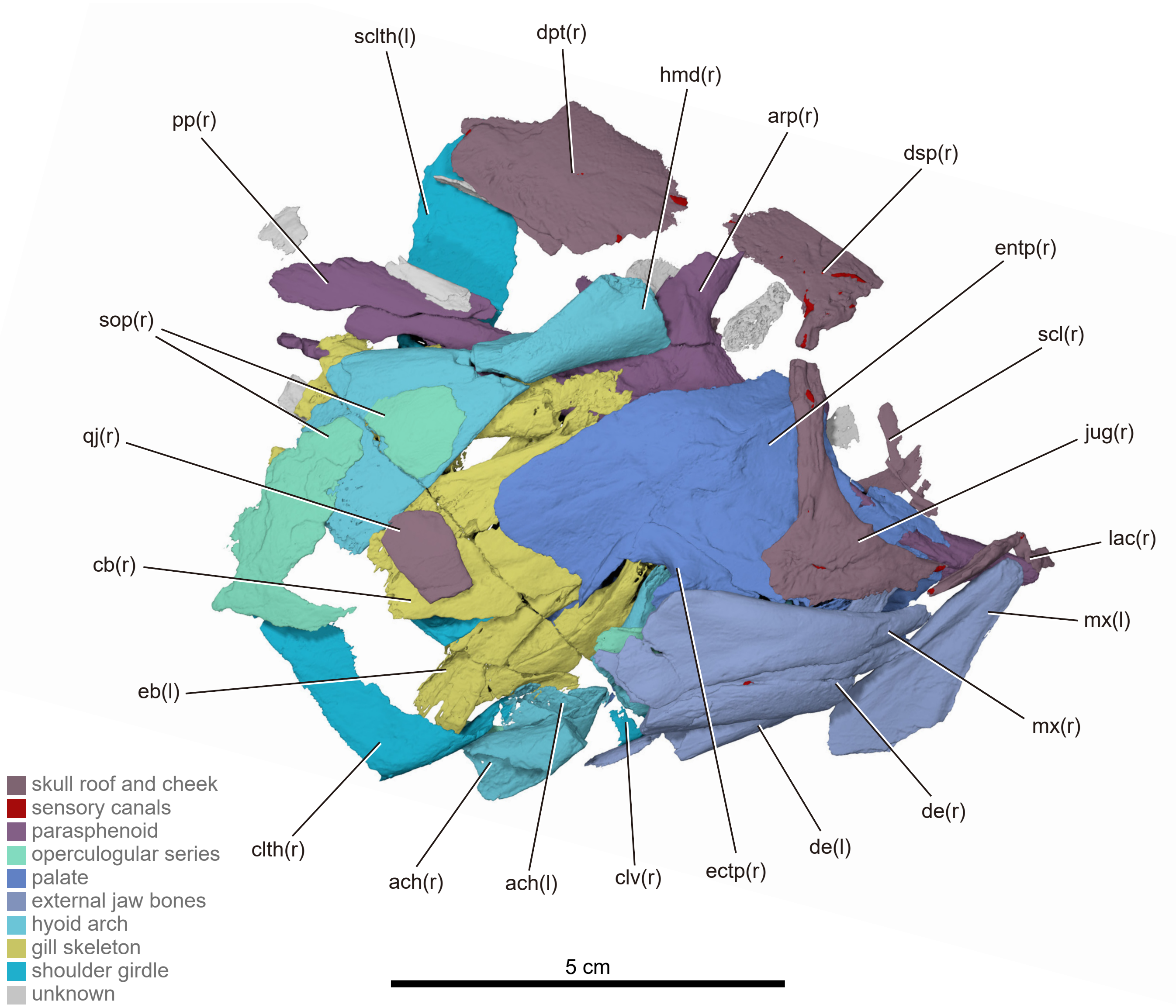


FIGURE 2 — †*Chondrosteus acipenseroides*, render of entire specimen (NHMUK PV P 75108) in right lateral view. Colors distinguish major anatomical regions as indicated in legend. Abbreviations: *ach*, anterior ceratohyal; *arp*, ascending process of parasphenoid; *clth*, cleithrum; *clv*, clavicle; *de*, dentary; *dpt*, dermopterotic; *dsp*, dermosphenotic; *eb*, epibranchial; *ectp*, ectopterygoid; *entp*, entopterygoid (= acipenseriform “palatopterygoid”); *hmd*, hyomandibula; *jug*, jugal; *lac*, lacrimal; *mx*, maxilla (= acipenseriform “dermopalatine”); *pp*, posterior process of parasphenoid; *qj*, quadratojugal; *scl*, scleral ossicle; *sclth*, supracleithrum; *sop*, subopercle. Suffixes (*r*) or (*l*) indicate right or left structure.

1989; Grande and Bemis, 1996). The jugal consists of a narrow vertical limb that expands ventrally, ending with a broad, fan-shaped expansion that widens further anteriorly than posteriorly. This gives it a clear anterior limb. Externally, the jugal bears a somewhat rugose ornament. The internal surface is smooth, interrupted by a distinct ridge that marks the course of the sensory canal; there is no medial process. The infraorbital canal (iocn, Fig. 4) enters the bone from its posterodorsal corner, then bends to extend ventrally to follow the course of the rod-like dorsal limb. It makes a sharp, right-angle bend in the expanded ventral portion of the jugal, extending anteriorly to continue to the lacrimal. No anterior branches of the main canal are apparent, but there are some posterior branches and numerous small, ventral ones.

The lacrimal is elongate and narrow (lac, Figs. 2–3), with its posterior portion overlapped by the jugal. It is

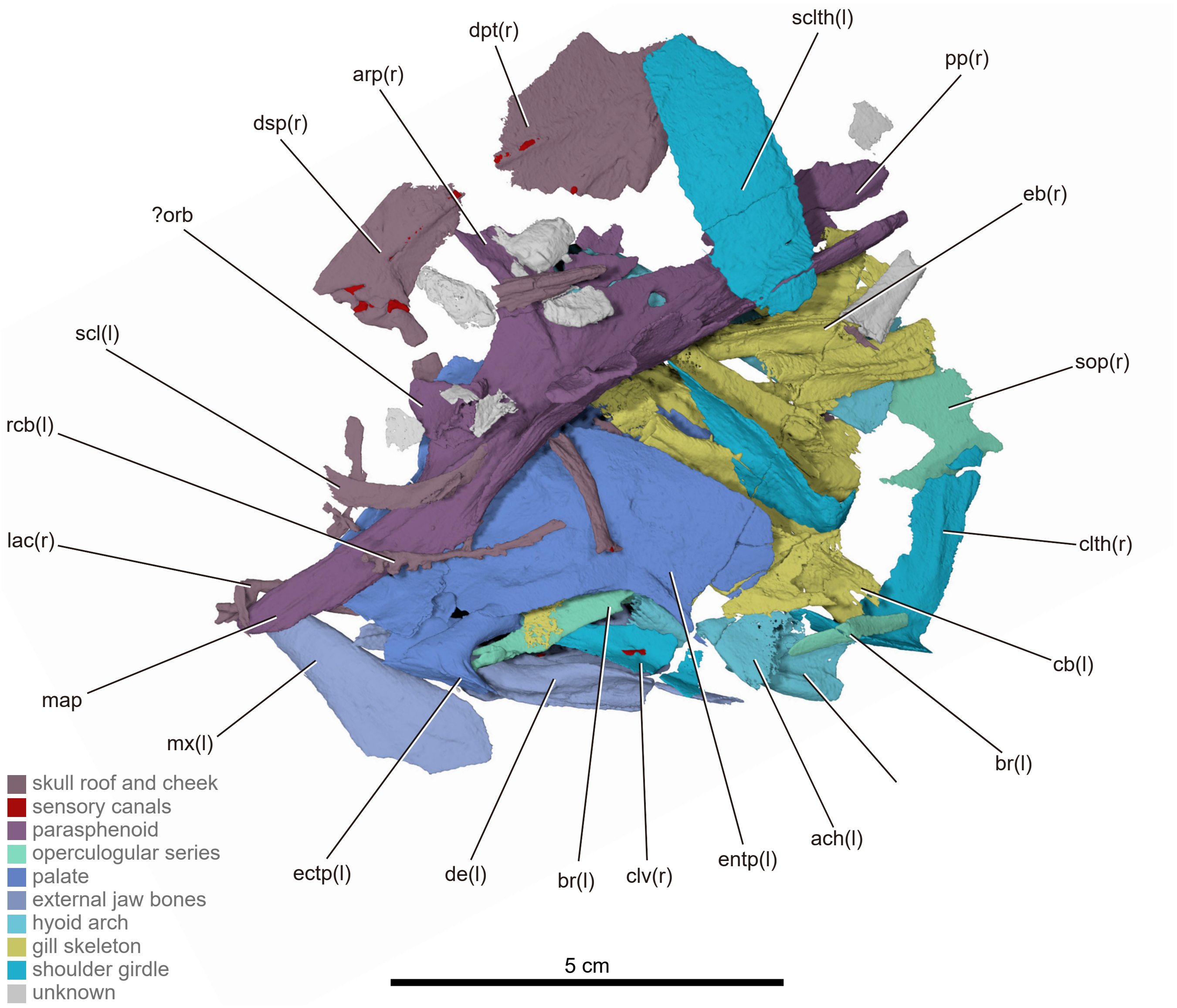


FIGURE 3 — †*Chondrosteus acipenseroides*, render of entire specimen (NHMUK PV P 75108) in left lateral view. Colors distinguish major anatomical regions as indicated in legend. Abbreviations: *ach*, anterior ceratohyal; *arp*, ascending process of parasphenoid; *br*, branchiostegal; *cb*, ceratobranchial; *clth*, cleithrum; *clv*, clavicle; *de*, dentary; *dpt*, dermopterotic; *dsp*, dermosphenotic; *eb*, epibranchial; *ectp*, ectopterygoid; *entp*, entopterygoid (= acipenseriform "palatopterygoid"); *lac*, lacrimal; *map*, median anterior process of parasphenoid; *mx*, maxilla (= acipenseriform "dermopalatine"); *?orb*, orbital ossification of braincase; *pp*, posterior process of parasphenoid; *rcb*, rostral canal bones; *scl*, scleral ossicle; *sclth*, supracleithrum; *sop*, subopercle. Suffixes *(r)* or *(l)* indicate right or left structure.

exposed on the surface of the specimen anteriorly and so may be incomplete due to breakage or historical preparation. The dorsal margin of the lacrimal is concave and forms the lower boundary of the orbit. Anteriorly, the lacrimal bends at a right angle then curves anteriorly, defining a distinctive kink (arc, Fig. 4). The infraorbital canal extends along the lacrimal and follows the shape of the bone, giving off small ramules laterally. This element may correspond to the posterior rostral canal bone of Hilton and Forey (2009: fig. 10A).

One identifiable scleral ossification (scl, Figs. 2–3) is present in each orbit. They are flat, narrow, gently curved. The left example is strongly distorted where it has been compressed against the parasphenoid. It is not possible to tell how many ossicles contributed to each complete ring, but the length and curvature of the preserved element suggests at least three or four were present.

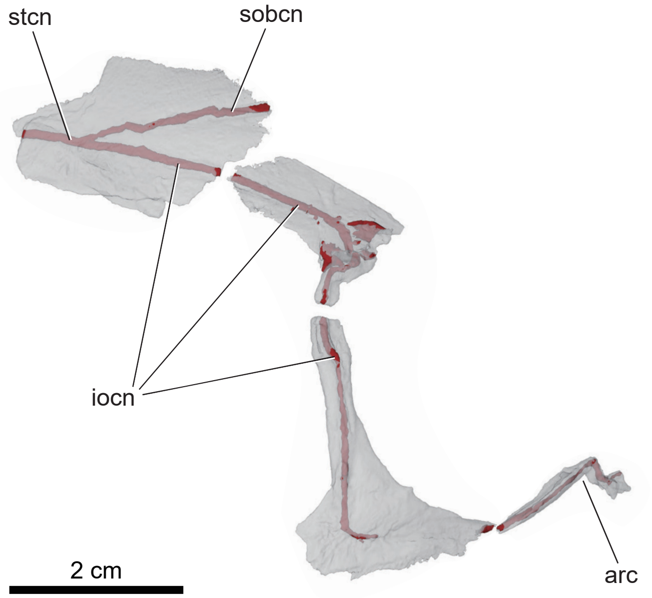


FIGURE 4 — †*Chondrosteus acipenseroides*, render of sensory canal patterns of the right lateral skull roof and cheek (NHMUK PV P 75108). Bones shown semitransparent to highlight path of the enclosed canals, which are rendered in red as in Figs. 2–3. Abbreviations: *arc*, arching of sensory canal; *iocn*, infraorbital sensory canal; *sobcn*, supraorbital sensory canal; *stcn*, supratemporal sensory canal.

Braincase Including Parasphenoid

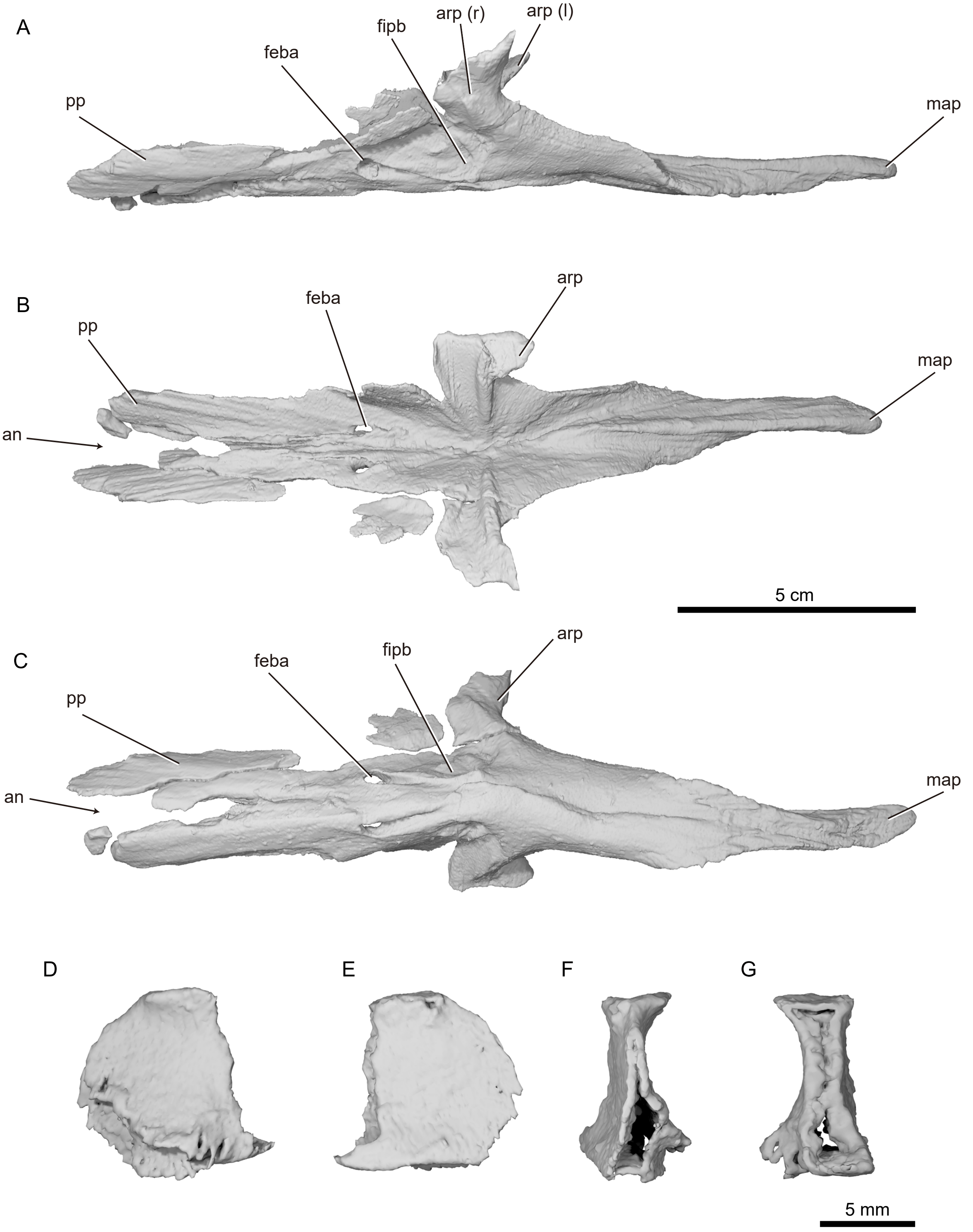
The large cruciform parasphenoid extends the length of the skull (Figs. 2–3, 5A–C). It can be roughly divided into three regions: an anterior sphenoid component, a middle region bearing the ascending processes, and a long posterior stalk. A spur-like median anterior process (map, Figs. 3, 5A–C) marks the anterior tip of the parasphenoid and likely reached the ethmoid region of the neurocranium. Dorsally, this process is continuous with a thick midline ridge on the upper surface of the parasphenoid that terminates just before the ascending processes. Posterior to the median process, the lateral margins flare dorsolaterally, giving the parasphenoid a trough- or gutter-like morphology that persists for the remainder of its length. There are no distinct dermal basipterygoid processes, but short ascending processes (arp, Figs. 2–3, 5A–C; ascending rami of Hilton et al. 2011) extend dorsally from the main body of the parasphenoid. Their anterior margins are reclined, giving the misleading impression in flattened material that the processes themselves are directed posteriorly (e.g., Hilton and Forey, 2009: 437). Each ascending processes bears an anteriorly directed extension at its dorsal end. Thickened ridges trace the anterior and posterior margins on the inner face of the ascending process and converge ventrally where it meets the main body of the parasphenoid. Posterior to the ascending process, the parasphenoid increases in height again before gradually shallowing, delineating a distinct notch in lateral view. A deep pit lying on the ventrolateral wall of the parasphenoid at the junction between the ascending process and posterior stalk likely represents the articular area for an infrapharyngobranchial (fipb, Fig. 5A, C). The long posterior stalk is incised on its ventral face by a deep groove, continuous with a large midline fenestra that is partially enclosed posteriorly. Behind this window, the parasphenoid bifurcates into two paired processes (pp, Figs. 2–3, 5A–C) bounding an aortic notch (an, Fig. 5B–C) that occupies roughly 20% of the overall length of the bone. A pair of large, anteriorly directed foramina for the efferent branchial arteries (feba, Fig. 5B–C) flank the anterior end of the midline groove of the parasphenoid. Each lies at the end of a deep trough that extends anteromesially to just behind the level of the ascending processes. The posterior extent of the parasphenoid relative to other parts of the skull is unclear, but it certainly continued to at least the hind margin of the operculogular series.

Several endoskeletal elements lie dorsal to the parasphenoid and represent components of an incompletely ossified braincase. The largest of these lies atop the basipterygoid region of the parasphenoid and is perichondrally ossified with minimal endochondral bone (?orb, Figs. 3, 5D–G). It is "C"-shaped in lateral view, with a straight posterior and curved anterior margin. In axial section, it flares slightly dorsally and ventrally, giving its lateral walls a gently concave profile. Based on its position and geometry, this might represent part of the orbital wall. However, it is unlike the orbitosphenoid of some extant acipenseriforms in lacking foramina for cranial nerves (Grande and Bemis, 1991; Findeis, 1993). Additional, apparently displaced, elements lie near the level of the ascending processes of the parasphenoid (gray elements in Figs. 2–3) but are harder to identify and interpret.

Operculogular Series

Only a partial subopercle and a few branchiostegals are preserved. The subopercle (sop, Fig. 2–3) is largely exposed on the surface of the specimen, with many of the margins therefore incomplete. A crack separates the anterodorsal corner from the main body. The branchiostegals (br, Fig. 3, 6) are elongate with triangular, medially tapering heads.

FIGURE 5 — (page 125) †*Chondrosteus acipenseroides*, renders of parasphenoid and neurocranial ossifications (NHMUK PV P 75108). Parasphenoid in: **A**, right lateral view; **B**, dorsal view; **C**, and ventral view. Orbital wall ossification in: **D**, medial; **E**, lateral; **F**, anterior; and **G**, posterior view. Abbreviations: *an*, aortic notch; *arp*, ascending process; *feba*, foramen for efferent branchial artery; *fibp*, facet for infrapharyngobranchial; *map*, median anterior process; *pp*, posterior process. Suffixes *(r)* or *(l)* indicate right or left structure where otherwise unclear.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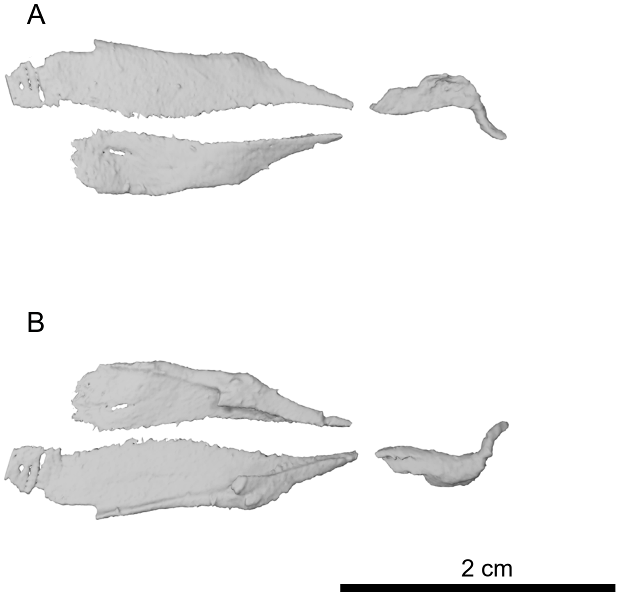


FIGURE 6 — †*Chondrosteus acipenseroides*, renders of branchiostegals (NHMUK PV P 75108). Select reassembled branchiostegals in: **A**, ventral and **B**, dorsal view. Anterior to right in both panels.

Their external surfaces are smooth and unornamented, with a raised rim on the ventrolateral margin of the inner face that is particularly pronounced in more ventral members of the series.

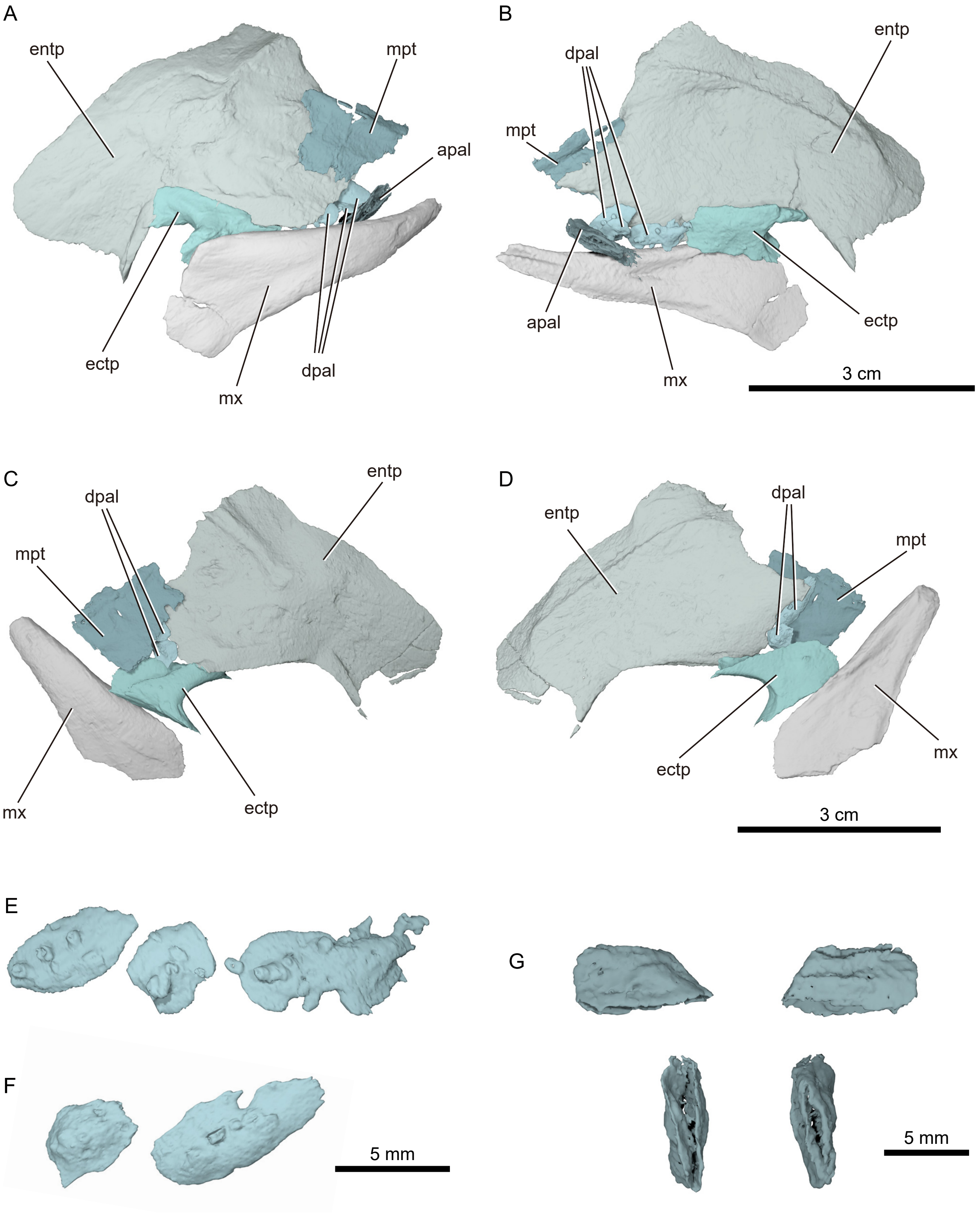
Palate and Upper Jaw

The upper jaw and palate and are best preserved on the right side of the skull. The most posterior parts of the upper jaw are incomplete, with an oblong, plate-like fragment representing a partial quadratojugal (qj, Fig. 2). This missing area is described and illustrated in several previous accounts of *Chondrosteus* (e.g., Traquair, 1887: fig. 4; Hilton and Forey, 2009: figs. 8, 11).

A kidney-shaped plate often called a palatopterygoid but corresponding to the entopterygoid of other actinopterygians (entp, Figs. 2–3, 7A–D; see Discussion) is the largest bone of the upper jaw. The entopterygoid extends the length of the upper jaws, from the level of the orbit anteriorly to just before the hyomandibula posteriorly. Its slightly convex aboral face has a rugose texture in places and bears a prominent anteroposteriorly directed ridge on its dorsal half. The oral surface of the entopterygoid is gently concave, with a broad groove along its thin posterodorsal edge. The ventral margin is thickened into a ridge that curves at a roughly 90 degree angle, resulting in a strong concavity in the lower edge of the entopterygoid. The posterior limb of this curve defines the rear margin of the adductor chamber while the anterior limb articulates with a series of additional bones. The most posterior of these is the short, topologically complex ectopterygoid (ectp, Figs. 2–3, 7A–D). Its medial arm forms a longitudinal trough, embracing the ventral margin of the entopterygoid with broad laminae that extend dorsally on both its lateral and medial faces. An anvil-shaped ectopterygoid process projects ventrolaterally, contacting the lateralmost dermal component of the upper jaw and defining the rounded anterior margin of the opening to the adductor fenestra. A series of three smaller bones, each ovoid with curved edges, articulate with the ventral margin of the entopterygoid anterior to the ectopterygoid on the right side of the skull (dpal, Fig. 7A–E). An incomplete series of two bones is preserved in the left jaw. In position, geometry, and number, they correspond to the dermopalatines of other actinopterygians; the better-preserved right examples are the basis of this description. The most posterior dermopalatine is the largest, with a length approximately that of the two more anterior ones combined. Teeth lie irregularly over its surface, with two closely spaced cusps on the posterior margin, three or four anteriorly directed crowns in the middle of the element, and one on the anterior margin. The central dermopalatine is the smallest of the series. Nearly circular in shape, it bears a row of three teeth, all of which point forward with the anterior crown the largest. These are joined by two isolated cusps, near the lateral and mesial margins of the bone. The anteriormost dermopalatine is elongate, with expansive smooth areas around all but the anterior margin. It bears three teeth, all similar in size, arranged in a row along midline.

Given the presence of conventional dermopalatines in †*Chondrosteus*, we interpret the large, splint-like dermal bone forming the lateral edge of the upper jaw as a maxilla (mx, Figs. 2–3, 7A–D, 8A–B; see Discussion). In lateral view, the toothless maxilla tapers gently anteriorly, with a straight dorsal and subtly sinusoid ventral margin. The latter results in a low, rounded extension of the ventral margin of the maxilla that overlaps the dentary as in “palaeonisciforms” (e.g., Gardiner, 1984; see also Hilton and Forey, 2009: figs 7, 11). However, the maxilla is not clearly differentiated into an anterior ramus and postorbital expansion as in generalized actinopterygians. Thickening of the dorsal and ventral edges relative to the rest of the maxilla is apparent in mesial view.

FIGURE 7 — (page 127) †*Chondrosteus acipenseroides*, renders of palate and upper jaw (NHMUK PV P 75108). Right palate and upper jaw in: **A**, lateral and **B**, medial view. Left palate and upper jaw in: **C**, lateral and **D**, medial view. Dermopalatines from: **E**, right (anterior to left) and **F**, left (anterior to right) jaws. **G**, autopalatine (handedness uncertain) showing completely finished surfaces (top row) and unmineralized ends (bottom row). Abbreviations: *apal*, autopalatine; *dpal*, dermopalatine; *ectp*, ectopterygoid; *entp*, entopterygoid (= acipenseriform “palatopterygoid”); *mpt*, metapterygoid (= acipenseriform “autopalatine”); *mx*, maxilla (= acipenseriform “dermopalatine”).


A
entp
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mpt
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F
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G
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The maxilla curves inward anteriorly, with the anterior tip missing in the specimen. Other material clearly shows the maxilla contributing to the upper jaw symphysis (e.g., Hilton and Forey, 2009: 439), but this is not apparent from our specimen. Posteriorly, the inner face of the maxilla abuts and is slightly underlain by the lateral arm of the ectopterygoid, suggesting the entire upper jaw and palate complex formed a tightly bound structure.

Two previously unreported endoskeletal bones contribute to the upper jaw of †*Chondrosteus*. The first of these is a thin, sheet-like rectangular ossification on the aboral surface of the palate corresponding to what is called an autopalatine in other acipenseriforms (mpt, Fig. 7A–D). It is best shown on the left side of the specimen, where it overlies the anterior end of the entopteryoid. The right example is badly broken where it has been compressed against the anterior region of the parasphenoid. The homologue of this bone is the only endoskeletal ossification of the anterior part of the upper jaw in other acipenseriforms where, as in †*Chondrosteus*, it consists of a thin sheet of perichondral bone termed an autopalatine (Grande and Bemis, 1991, 1996; Hilton et al., 2011). We interpret this element as a metapterygoid (Tsessarsky, 2024; see Discussion). The second endoskeletal bone is preserved only on the right side of the specimen, where it is displaced anteroventral to the demopalatines (apal, Fig. 7A–B,G). It is smaller but substantially more robust than the metapterygoid, with a trapezoidal profile. Rather than being sheet-like, it is instead a stout ossification consisting of an outer sleeve of perichondral bone enclosing sparse endochondral trabeculae. The two longest margins of the bone are unfinished, indicating articular surfaces. In terms of relative size (smaller than other palatal bones), position (at the anterior end of the palate), and overall morphology (stout and trapezoidal), this bone agrees with the autopalatine of several living and extinct actinopterygians (Arratia and Schultze, 1991: figs. 34–35; Friedman et al., 2024: fig. 12B–C; Cavicchini et al., 2025: fig. 8A–B; see Discussion).

Lower Jaw

The toothless mandible consists only of a dentary externally and a prearticular lining its medial face. There is no indication that any part of the Meckelian cartilage was ossified in this specimen, although it is reported in other individuals (Hilton and Forey, 2009: fig. 12). A conspicuous longitudinal groove divides the narrow, elongate dentary (de, Figs. 2–3, 8) into distinct dorsal and ventral portions. A few widely spaced canals extend from this gutter to open on the inner face of the dentary, marking the path of nerves for the unenclosed mandibular sensory canal. The upper portion of the dentary

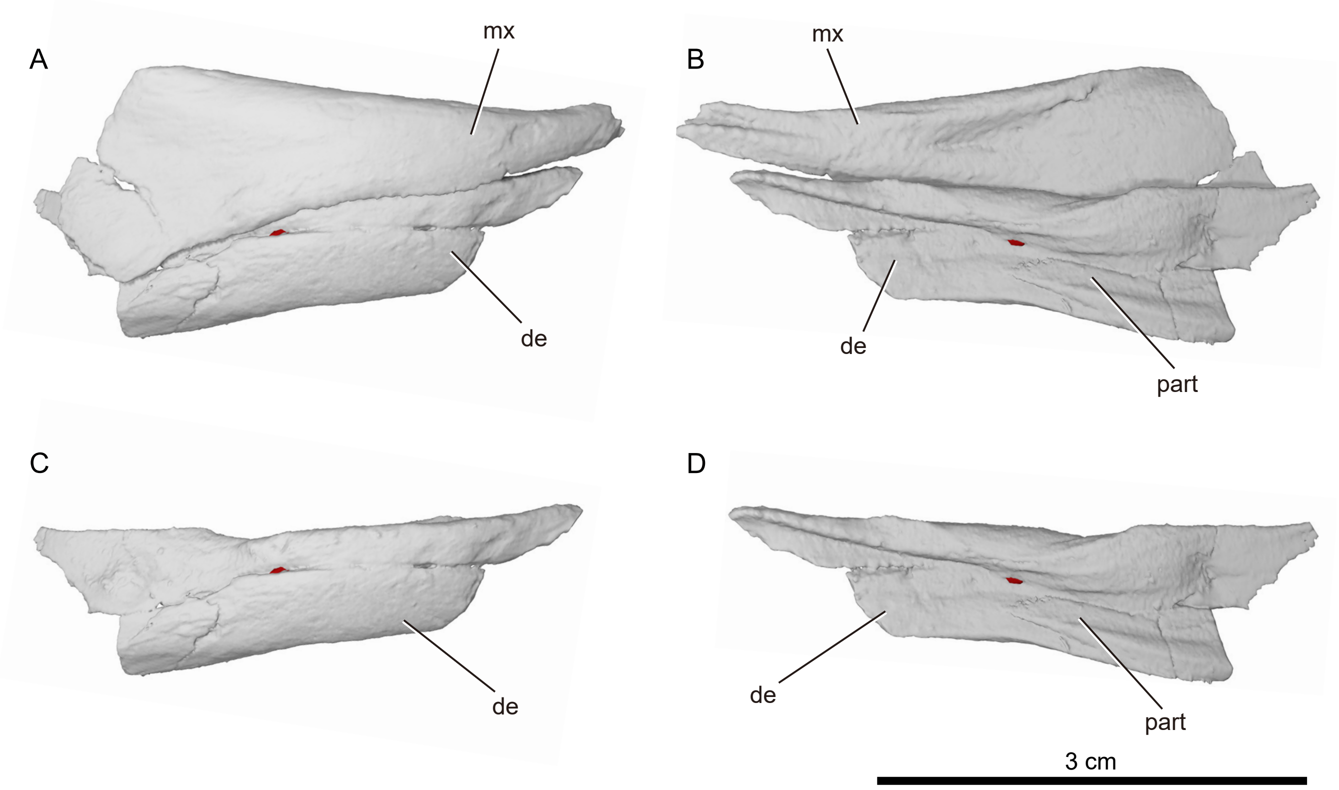

FIGURE 8 — †*Chondrosteus acipenseroides*, renders of right upper and lower jaw (NHMUK PV P 75108). Right upper and lower jaw in: **A**, lateral and **B**, medial view. Right lower jaw in: **C**, lateral and **D**, medial view. Red indicates sensory canal. Abbreviations: *de*, dentary; *mx*, maxilla (= acipenseriform "dermopalatine"); *part*, prearticular.

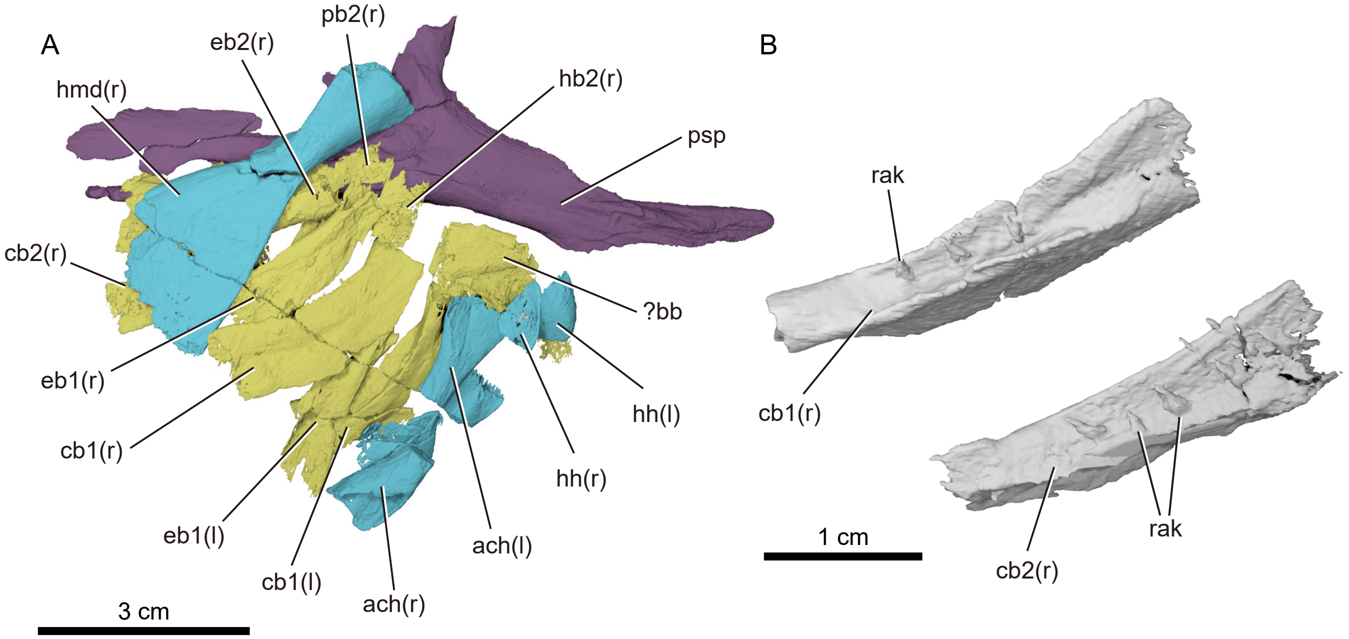

FIGURE 9 — †*Chondrosteus acipenseroides*, renders of parasphenoid, hyoid and branchial skeleton (NHMUK PV P 75108). **A**, components as preserved in right lateral view. **B**, gill rakers on ceratobranchials. Color coding in panel A as in Figs. 2–3. Abbreviations: *ach*, anterior ceratohyal (gap corresponds to fracture in specimen); ?*bb*, possible basibranchial; *cb*, ceratobranchial; *eb*, epibranchial; *hb*, hypobranchial; *hh*, hypohyal; *hmd*, hyomandibula; *rak*, raker; *pb*, pharyngobranchial; *psp*, parasphenoid. Suffixes *(r)* or *(l)* indicate right or left structure; numerical suffixes indicate position of an element within a set of serial homologues.

expands and flattens posterodorsally. This wing corresponds to the area of the adductor fossa and bears a slight depression to accommodate the overlapping maxillary flange. In dorsal view, the dentary is sinusoid, curving slightly medially toward its anterior tip. Its upper margin is thin posteriorly, expands substantially in the middle part of the bone, and tapers again toward the symphysis. The inner surface of the dentary is concave, with a pronounced inturned ridge along the dorsal margin in the anterior third of the bone. The narrow splint-like prearticular (part, Fig. 8B, D) tapers anteriorly and is preserved in close association with the inner face of the right dentary. Its dorsal and ventral margins are thicker than the body of the bone.

Hyoid Arch

The hyoid arch is best preserved on the right side of the specimen and includes an ossified hyomandibula, ceratohyal, and hypohyal. The imperforate hyomandibula (hmd, Figs. 2, 9A, 10) is large and flat. It may have undergone some level of lateral compression, especially in its posterior half where perichondral ossification is thin. A strong constriction at midlength gives the hyomandibula a waisted or hourglass-shaped profile, with the distal end broader than the proximal one. There is no opercular process. A ridge extends along the medial surface of the hyomandibula, but its lateral face is smooth. A broad gap, presumably bridged by additional hyoid cartilages, lies between the distal end of the hyomandibula and the short anterior ceratohyal (ach, Figs. 2–3, 9A, 10). It is taphonomically flattened but retains an attenuated hourglass shape with expanded anterior and posterior ends. A break in the specimen extends through the middle constricted region of the anterior ceratohyal, separating the bone in two. A triangular hypohyal (hh, Fig. 9A, 10) lies anterior to the anterior ceratohyal and bears a thin sheath of perichondral bone.

Branchial Arches

The branchial skeleton is incompletely preserved, with the right side being substantially more intact. Compression and taphonomic disruption, with the associated loss of positional information, makes interpretation of individual bones challenging. Portions of four arches appear to be preserved, with varying degrees of completeness. Of the ventral gill skeleton, only the ceratobranchials (cb, Figs. 3, 9–10) can be confidently identified. Ceratobranchial 1 is large, roughly half the length of the hyomandibula, with a stout perichondral coat. It is gently curved, with a concave dorsal and convex ventral margin, and has flat distal and proximal ends. The lateral surface of ceratobranchial 1 bears a longitudinal groove that opens dorsally and contains a series of at least three broadly spaced, finger-like rakers (rak, Fig. 9B). The smaller

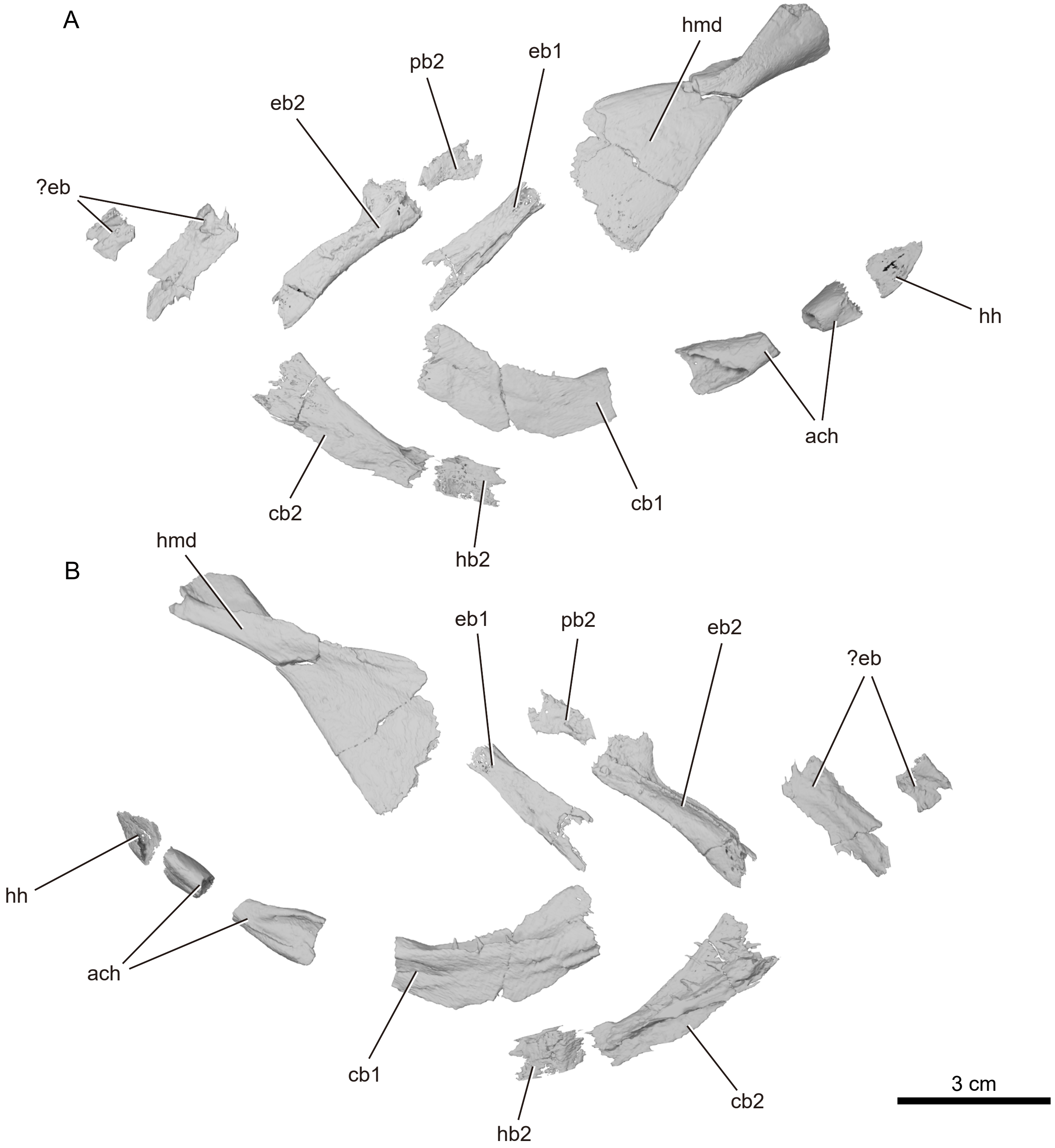

FIGURE 10 — †*Chondrosteus acipenseroides*, renders of hyoid and branchial skeleton (NHMUK PV P 75108). Pulled-apart components of right branchial and hyoid arches in: **A**, lateral and **B**, medial view. Abbreviations: *ach*, anterior certoyhal; *cb*, ceratobranchial; *eb*, epibranchial; *hb*, hypobranchial; *hh*, hypohyal; *hmd*, hyomandibula; *pb*, pharyngobranchial. Numerical suffixes indicate position of an element within a set of serial homologues.

ceratobranchial 2 is more slender than from the first member of the series, with less severely curved margins. It bears at least five rakers in a deep longitudinal sulcus, as well as at least two smaller rakers on its dorsolateral margin. A poorly ossified possible hypobranchial is associated with the anterior margin of right ceratobranchial 2. Larger, perichondrally ossified elements at the anterior margin of the branchial skeleton are crushed flat and may represent basibranchials (?bb, Fig. 9A).

FIGURE 11 — †*Chondrosteus acipenseroides*, renders of ventral right shoulder girdle (NHMUK PV P 75108). Red indicates canal. Cleithrum in: **A**, lateral; **B**, mesial; and **C**, anterior view. Clavicle in: **D**, lateral; **E**, medial; and **F**, ventral view.

The dorsal gill skeleton is represented by epibranchials (eb, Figs. 2, 9A, 10) and pharyngobranchials (Figs. 9A, 10). Epibranchial 1 is preserved on both the right and left sides of the specimen. This rod-like bone bears a longitudinal groove that extends along its dorsal surface. Epibranchial 2 is preserved only on the right side of the specimen, is shorter than epibranchial 1, and distinguished from it by a low but broad uncinate process. Its proximal end articulates with a poorly mineralized infrapharyngobranchial lying just posterior to the pharyngobranchial articular pit on the parasphenoid. At least two additional branchial elements are preserved posterior and dorsal to epibranchial 2 but are truncated posteriorly by the break of the specimen and their identity is therefore difficult to determine. They may be fragments of epibranchials (?eb, Fig. 10).

Pectoral Girdle

The shoulder girdle is incompletely preserved, represented by partial right and left cleithra, a mostly complete right clavicle, and a complete left supracleithrum. The cleithrum (clth, Figs. 2–3, 11) consists of a tall vertical arm composed of a externally facing lamina with a gently concave lateral surface. Ventrally, this arm is joined to a smaller, medially directed lamina ventrally. This lamina extends anteriorly beyond the level of the dorsal arm, producing an anterior projection that gives the cleithrum an "L"-shaped profile in lateral view. The supracleithrum (sclth, Figs. 2–3) is lozenge shaped, and slightly longer than the dorsal lamina of the cleithrum. Its anterior and posterior margins are approximately parallel, and it does not narrow ventrally. An elongate, narrow element that tapers anteriorly lies some way in front of the cleithra, between the branchiostegals (clv, Figs. 2–3, 11). It consists of lateral and ventral laminae at right angles to each other. Each lamina is pierced by a canal, with the canal on the lateral face larger and extending into a groove on the medial surface of the element. As the shape and curvature of the inner surface of this element corresponds closely to the external surface of the ventral part of the cleithrum, we identify it as a clavicle.

DISCUSSION

μCT examination of NHMUK PV P 75108 corroborates aspects of †*Chondrosteus* reported by Hilton and Forey (2009), and we find no major discrepancies with the anatomy presented in that contribution. Significantly, we can identify structures that are either poorly exposed or not visible in other material. This, in turn, has implications for the homology of some bones between acipenseriforms and other actinopterygians, particularly with respect to the upper jaw. Our new observations of †*Chondrosteus* bear on conditions that may be plesiomorphic for acipenseriforms and are thus relevant for future work looking to determine which other extinct actinopterygians might belong to the acipenseriform total group. As additional context, we review candidates that have been advanced in the past as possible relatives of acipenseriforms.

New Insights on the Cranial Anatomy of †*Chondrosteus*

Our novel observations of †*Chondrosteus* pertain mostly to aspects of internal anatomy inaccessible to earlier researchers. In some instances, these suggest revised character-state scorings for †*Chondrosteus*. We note changes by parenthetically citing character numbers and states (in the format [previous state → revised state]) from Hilton and Forey (2009). Although these revised states might change inferences of character polarity for crown acipenseriforms, they do not appear to refute the placement of †*Chondrosteus* outside that group. First, we confirm the presence of a median anterior process of the parasphenoid in †*Chondrosteus*. This feature is sporadically distributed among acipenseriforms, and Hilton and Forey (2009: 437) were only able to identify it in †*Chondrosteus* with "a moderate degree of confidence." Second, we find that in the unflattened parasphenoid of NHMUK PV P 75108 the ascending processes are directed perpendicular to the main body of the bone as in polyodontids. This contrasts with the posteriorly directed orientation indicated by past work, which we attribute to distortion arising from taphonomic flattening (Hilton and Forey, 2009: character 16 [1 → 0]). Third, we find evidence for limited mineralization of the neurocranium in †*Chondrosteus* in the form of isolated bones in the sphenoid and otic regions. Although these are not clearly identifiable, they suggest a pattern of separate, small ossification centers in †*Chondrosteus* comparable to that of some extant acipenseriforms (Grande and Bemis, 1991; Hilton et al., 2011). Fourth, we confirm absence of a medial process of the jugal (Hilton and Forey, 2009: character 8 [? → 0]). Fifth, we identify a lacrimal with a distinctively kinked profile, giving the rostral sensory canal a strong bend (Hilton and Forey, 2009: character 11 [? 1]). This character has previously been considered an acipenserid synapomorphy, unknown in †*Chondrosteus* (Findeis, 1997; Hilton et al., 2011). The condition in extant acipenserids is, however, more extreme: a distinct lacrimal is not apparent, and instead many small ossicles carry the canal anterior to the jugal, extending along the ventral, rather than lateral, surface of the snout. The strong curve of the canal in acipenserids accommodates the lateralmost set of barbels. Sixth, we provide greater detail on the gill skeleton, including confident identification of some bones of the dorsal series. In extinct acipenseriforms, epibranchials have only been described for †*Crossopholis* (Grande and Bemis, 1991: fig. 57) and †*Priscosturion* (Grande and Hilton, 2006: figs 12, 20), although some also appear to be present—but not identified—in †*Anchiacipenser* (Sato et al., 2018: fig. 7). In the Cretaceous acipenserids, ossification appears restricted to the midsection of the bones, leaving long unmineralized distal and proximal ends (cf. *Scaphirhynchus platorynchus*; Findeis, 1993: fig. 30). This stands in contrast to what appears to be mineralization along much of the length of the epibranchials in †*Crossopholis* and †*Chondrosteus*.

These incremental adjustments to our understanding of the anatomy of †*Chondrosteus* are contrasted with significant

TABLE 2 — Review of proposed homologies of bones contributing to the upper jaw in †*Chondrosteus acipenseroides*. Identifications given by Grande and Bemis (1996) and Hilton and Forey (2009) follow the homologies proposed for acipenseriforms by Findeis (1993) and applied to most subsequent work on extinct and extant members of the group. The em-dash (—) indicates a component of the upper jaw not reported in the study. Asterisk (*) indicates this bone is reported in other acipenseriforms by these authors as an autopalatine.

this study	dermopalatines	ectopterygoid	entopterygoid	maxilla	quadratojugal	metapterygoid	autopalatine
Grande and Bemis (1996); Hilton and Forey (2009)	—	ectopterygoid	palatopterygoid	dermopalatine	quadratojugal	— *	—
Gardiner and Schaeffer (1989)	—	—	pterygoid	maxilla	preoperculum	—	—
Woodward (1895)	—	palatine or ectopterygoid	pterygoid	maxilla	jugal	—	—
Traquair (1887)	—	pterygoid	mesopterygoid	maxilla	jugal	—	—
Davis (1887)	—	maxilla (part)	palatine	maxilla (part)	maxilla (part)	—	—
Egerton (1858)	—	maxillary	premaxillary	epibranchial	—	—	—

revisions related to the structure of the upper jaw. We identify a series of tooth-bearing bones along the ventrolateral margins of the palate plus two endoskeletal ossifications lying on its aboral surface. These have implications for the homologies of upper jaw bones in †*Chondrosteus* and acipenseriforms more generally, which we consider in the following section (proposed homologies summarized in Table 2).

Homologies of the Upper Jaw Bones in †*Chondrosteus* and Other Acipenseriforms

Dermal Upper Jaw.— Prior to our µCT re-examination, the upper jaw of †*Chondrosteus* was considered to contain four distinct dermal ossifications (names applied by Hilton and Forey, 2009 given in parentheses): a broad plate-like bone forming the roof of the mouth (palatopterygoid), a strap-like bone forming the lateral edge of the jaw (dermopalatine), a stocky, columnar ossification uniting these previous two bones in the middle of the jaw (ectopterygoid), and an elongate plate-like bone at the posterior end of the jaw (quadratojugal). Traquair (1887: fig. 4) arrived at an essentially modern interpretation of the structure and composition of the upper jaw of †*Chondrosteus* following confusion among earlier researchers. Egerton (1858: 878) only attributed two bones to the upper jaw and regarded the bone forming its lateral edge as an epibranchial. Davis (1887: 612) identified the large plate-like palatal bone and regarded the three more lateral components recognized by Traquair (1887) and later workers as one large, continuous "C"-shaped maxilla. Additionally, Davis (1887) mentioned a premaxilla but did not figure or otherwise describe it; it is unclear from his text if this premaxilla was merely inferential or was informed directly by some aspect of the anatomy of his specimen.

The four large dermal bones of the upper jaw in †*Chondrosteus* match, in broad details of their structure and arrangement, what is found in other acipenseriforms. The principal contrasts lie with polyodontids, where the more anterior bone (ectopterygoid) bridging the lateral splint and the broad plate roofing the mouth is never present as a separate ossification (Grande and Bemis, 1991; Grande et al., 2002). *Polyodon* itself is more extreme in additionally lacking the posterior bridging bone (quadratojugal). By the first half of the 20th century, a stable nomenclature emerged for acipenseriform upper jaw bones (MacAlpin, 1947), largely matching Traquair's (1887) earlier identifications in †*Chondrosteus*: a large pterygoid (or later palatopterygoid; Jollie, 1980) joined to a lateral maxilla by an ectopterygoid anteriorly and a quadratojugal posteriorly. Even before this nomenclature stabilized for other component bones, there was widespread agreement that the most lateral component of the acipenseriform upper jaw was, as in other actinopterygians, a maxilla (Parker, 1882; Sewertzoff, 1926, 1928; Gregory, 1933). Although he accepted this identification, Jollie noted that "[t]he maxilla of this group [acipenseriforms] is also peculiar in its close relationship to the margins of the palatoquadrate; in most forms the maxilla lies well lateral in the mouth margin although there is some contact with the anterior and the cartilage" (1980: 237). This statement rests on the pattern of upper jaw construction in extant neopterygians (e.g., Grande and Bemis, 1998; Grande, 2010), in contrast to the intimate association apparent between the palate and maxilla found in many extinct taxa from the Paleozoic and early Mesozoic (Watson, 1925; Nielsen, 1942; Gardiner, 1984; Giles et al., 2015). Jollie's (1980) observation was carried further by Findeis, first in a conference abstract (Findeis, 1991) and then later in his dissertation (Findeis, 1993). There he noted that "development of this bone [the maxilla of earlier authors] in *Scaphirhynchus platorynchus* is intimately associated with the palatoquadrate . . . suggesting that it is actually a palatoquadrate investing bone, *and hence a dermopalatine*" (Findeis, 1993: 297; emphasis ours). This interpretation became widely adopted in subsequent descriptive accounts of acipenseriforms over the next few decades (Grande and Bemis, 1996; Bemis et al., 1997; Grande et al., 2002; Grande and Hilton, 2006; Hilton and Forey, 2009; Hilton et al., 2011, 2016, 2020, 2021, 2023; Warth et al., 2017, 2018; Sato et al., 2018; Hilton and Grande, 2023), with particularly detailed argumentation provided by Grande et al. (2002: 225).

However, Datovo and Rizzato (2018: 25–26, fig. 11) dissented from this established view. In their examination of facial muscle evolution in actinopterygians, they noted two major inconsistencies with the dermopalatine hypothesis: contrasting development of the acipenseriform "dermopalatine" compared to that of other taxa, and the otherwise unprecedented extension of this putative "dermopalatine" lateral to the jaw adductor musculature. The classic interpretation of the bone, Datovo and Rizzato (2018) argued, was more parsimonious, requiring only loss of the dermopalatines in acipenseriforms rather than loss of the maxilla combined with developmental and anatomical reconfiguration of the dermopalatine. In a series of papers, Tsessarsky (2020, 2024) further amplified this argument, noting similarities between the acipenseriform "dermopalatine" and maxillae of other actinopterygians, as well as additional developmental differences between it and unambiguous dermopalatines. More recent descriptive work on extinct (Hilton et al., 2021, 2023; Hilton and Grande, 2023) and extant (Hilton et al., 2020) acipenseriforms maintain the terminology of Findeis for consistency, while indicating that other names might more accurately reflect homologies (Hilton et al., 2020: 64).

The homologies reinstated by Datovo and Rizzato (2018) and Tsessarsky (2020, 2024) indicate that extant acipenseriforms lack dermopalatines, with the implication that these bones may be present in earlier members of the lineage. Although obscured from external examination, our µCT data reveal a series of two or three rounded dermal bones belonging to the palate that have not previously been reported for †*Chondrosteus*. These correspond in position (anterior to ectopterygoid, ventral to the entopterygoid), structure (tooth-bearing), relative size (smaller than other dermal components of the palate), and number (several) to the dermopalatine series of early actinopterygians like †*Mimipiscis* (Gardiner, 1984: figs 53–54; see also Arratia and Schultze, 1991). The examples in †*Chondrosteus* differ in not being tightly sutured to one another or to other bones of the upper jaw, but we interpret this as reflecting the general reduction of the dermal skeleton. Small, discontinuous, and developmentally ephemeral tooth-bearing plates have recently been identified in association with the second hypobranchial of larval sterlet sturgeon (*Acipenser ruthenus*; Pospislova et al., 2021: figs. 5L, 7C, F). These bear a general morphological similarity to the elements we identify as dermopalatines in †*Chondrosteus*. However, we note two lines of evidence refuting a hypobranchial association for these newly recognized plates. First, the bones in †*Chondrosteus* are in line with the anteroventral margin of the entopterygoid and distant from the gill skeleton, which has been displaced en masse posterodorsally and away from the tooth plates themselves. Second, the teeth borne by the plates in †*Chondrosteus* point ventromedially towards the opposing palate rather than anterodorsally to oppose the roof of the mouth as in the sterlet (Pospislova et al., 2021: fig. 9A). Our identification of these elements as dermopalatines is not without precedent. Watson (1928) highlighted a specimen of †*Chondrosteus* as showing "two small elements lying in the specimen rather in front of, though in the same plane as, the pterygoid, which are more plausibly interpreted as reduced palatine bones" (1928: 69). We are uncertain as to the whereabouts of Watson's unnumbered fossil, but his somewhat schematic illustration shows two bones roughly comparable in relative size to the dermopalatines of NHMUK PV P 75108 (Watson, 1928: fig. 15). Watson's earlier account of †*Chondrosteus* illustrates another specimen with two bones lying on the oral surface of the anatomically left entopterygoid along its anterolateral margin (Watson, 1925: fig. 7). These were unidentified in this account, but Watson (1928) later interpreted them as palatines to match his new observations. Several displaced tooth plates are indicated in the branchial region of multiple specimens of †*Chondrosteus* by Hilton and Forey (2009: 439), and it is unclear if these are associated with the gill arches or could belong to the palate.

The dermopalatines of †*Chondrosteus* occur in conjunction with the lateral, strap-like "dermopalatine" of Findeis (1993) and others, decisively rejecting the hypothesized homology of the latter (Patterson, 1982b, 1988). Instead, the resurrected identification of this marginal bone as a maxilla by Datovo and Rizzato (2018) and Tsessarsky (2020, 2024) appears to be correct. This will have implications for how characters relating to the maxilla and dermopalatines are applied to acipenseriforms in broader surveys of actinopterygian phylogeny; most current phylogenetic analyses code the maxilla as absent in taxa such as *Acipenser* and †*Chondrosteus* (e.g., Cloutier and Arratia, 2004; Giles et al., 2023). Confirmation of a maxilla in acipenseriforms should also prompt a reconsideration of the fate of the premaxilla, which is absent in all living and extinct acipenseriforms. Although early developmental studies of *Acipenser* suggested that the maxilla developed from two tooth-bearing precursors, the anterior of which was interpreted as the remnant of a premaxilla (e.g., Sewertzoff, 1928: 465), this hypothesis does not appear to be corroborated by more recent work (e.g., Pospisilova et al., 2021; Tsessarsky, 2024)

The presence of independent dermopalatines in †*Chondrosteus* invites new interpretation of palatal teeth reported in some other acipenseriforms. Particularly relevant are conditions in some polyodontids. In *Polyodon*, Grande and Bemis (1991: 25) report "a long, multiple-rowed patch of teeth in young specimens (50 to 400 mm) that resembles a long tooth plate fused to the [entopterygoid, their palatopterygoid] bone." This toothed field, which apparently does not develop as an autogenous structure, extends along the ventral margin of the anterior half of the entopterygoid in the position of the dermopalatines of other actinopterygians. In their review of ossifications associated with the osteichthyan palatoquadrate, Arratia and Schultze (1991: 55) considered this structure in *Polyodon* to be a fused dermopalatine. A similar dentigerous patch is present as a separate ossification in †*Crossopholis*, where it can be observed disassociated from other bones of the upper jaw (Grande and Bemis, 1991: fig. 65B). The condition in the Cretaceous stem polyodontid †*Protopsephurus* is unclear, with specimens figured by Grande et al. (2002: figs 6-8, 11) only showing the dorsolateral surface of the upper jaws. The surface of the upper jaws is obscured by matrix in the only specimen of †*Paleopsephurus* (MacAlpin, 1947: figs 7-8; Grande and Bemis, 1991: fig. 69), but µCT scans of UMMP VP 22206 (data provided in Table 1) show no evidence of dentition. Dermopalatines also appear to be absent in the †peipiaosteids †*Yanosteus* (Hilton et al., 2021: fig. 4) and †*Peipiaosteus* (Grande and Bemis, 1996: fig. 6; Jin, 1999: fig. 4). At present, it is more parsimonious to interpret the palatal tooth fields and plates of †*Crossopholis* and *Polyodon* as reacquired rather than retained (and, in *Polyodon*, subsequently fused to the entopterygoid; Arratia and Schultze, 1991) dermopalatines.

In addition to this revised interpretation of the acipenseriform "dermopalatine", we accept the proposed identification of the large, plate-like bone of the palate in acipenseriforms as the entopterygoid (Tsessarsky, 2020, 2024), rather than the more general pterygoid (Arratia and Schultze, 1991) or clade-specific palatopterygoid (Jollie, 1980). Like the ectopterygoid of other actinopterygians (Arratia and Schultze, 1991), that of †*Chondrosteus* lines the inner surface of the palatoquadrate and contacts both the entopterygoid and dermopalatines ventrally.

Endoskeletal Upper Jaw.— Endoskeletal ossifications of the upper jaw have not been reported previously for †*Chondrosteus*. We find evidence of two bones: a larger perichondral sheet that lies over the anterior part of the aboral surface of the entopterygoid, and a smaller, but more robustly constructed, ossification that lies anteroventral to the entopterygoid. The arrangement in †*Chondrosteus* is significant because no other acipenseriform has multiple endoskeletal ossifications contributing to the anterior part of the upper jaw (some extant acipenseriforms have a mineralized quadrate; Hilton et al., 2011). The larger of the two bones clearly corresponds to what is conventionally identified as an autopalatine in other acipenseriforms, where it is typically only present in larger individuals (Grande and Bemis, 1991; Hilton et al., 2011). The second, smaller bone has no obvious equivalent in other acipenseriforms, either extinct or living. If identification of the larger ossification as an "autopalatine" is correct, the position and structure of the smaller bone is not easily reconciled with what is known of ossification patterns of the osteichthyan palatoquadrate (Arratia and Schultze, 1991).

Tsessarsky's (2024) evaluation of bone identities in acipenseriforms provides a possible solution to this puzzle. He interprets the sheet-like acipenseriform "autopalatine" as a metapterygoid. This is based principally on patterns of soft-tissue connection to the neurocranium. Primitively in bony fishes, the metapterygoid (or the pars metapterygoidea when separate ossifications are not present; Arratia and Schultze, 1991) participates in the palatobasal articulation via direct connection to the neurocranium. Osteological markers for this attachment in early actinopterygians include a fenestra in the pars metapterygoidea and a prominent basipterygoid process on the braincase (Gardiner, 1984). This arrangement is modified to varying degrees among extant taxa, with acipenseriforms lacking any direct skeletal contact between the upper jaw and the neurocranium. However, acipenseriforms do have a ligamentous sheath connecting the palate with the braincase that is presumably related to the ancestral skeletal palatobasal articulation (De Beer, 1925: 678, fig. 10). This ligament extends from below the orbit to include the region of the upper jaw occupied by the "autopalatine", suggesting this is probably the metapterygoid (Tsessarsky, 2024). The smaller, more robust endoskeletal palatal bone in †*Chondrosteus* can therefore be interpreted as an autopalatine, an interpretation bolstered by structural similarities with the autopalatines of extant taxa like *Amia* and *Polypterus* (Arratia and Schultze, 1991: figs 34–35). These identifications in †*Chondrosteus* also draw some support from comparisons with separate palatoquadrate ossifications in early actinopterygians. While many "palaeonisciforms" have a single mineralized palatoquadrate (Gardiner, 1984; Giles et al., 2015), a handful have separate autopalatine, metapterygoid, and quadrate ossifications (†*Daemodontiscus*: Friedman et al., 2024: fig. 12B–C; †*Pteronisculus*: Cavicchini et al., 2025: fig. 8A–B).

Implications for Acipenseriform Jaw Evolution and Function.— The feeding structures of living acipenseriforms are highly specialized, reflecting substantial architectural modifications that permit protrusion of the entire mandibular arch (Carroll and Wainwright, 2003). Given the broad structural outlines available to earlier workers, the upper jaw morphology of †*Chondrosteus* appears at first glance to be essentially like that of living sturgeons and paddlefishes. Consequently, it might be assumed that the distinctive acipenseriform jaw function characterized even the earliest members of the group. While our new data do not radically alter the overall geometry and principal components of the upper jaw of †*Chondrosteus*, which have both been more-or-less clear since Traquair (1887), the recognition of bones previously thought lost in this genus and other acipenseriforms have two important consequences. First, these retained ossifications reinforce the hypothesized phylogenetic placement of †*Chondrosteus* as part of the sister-group of all other recognized acipenseriforms. Second, the "intermediate" jaw morphology of †*Chondrosteus* further atomizes the sequence of modifications leading to the condition in extant sturgeons and paddlefishes. As in generalized actinopterygians, †*Chondrosteus* retains endoskeletal ossification of the autopalatine and autogenous toothed dermopalatines, which presumably had implications for jaw suspension (autopalatine) and prey capture and retention (dermopalatines). This raises questions about jaw function in the earliest recognized acipenseriforms, especially the degree to which the protrusion so characteristic of living forms was possible. Although the sparse anatomical detail available in the past has invited the projection of contemporary acipenseriform features upon †*Chondrosteus* (e.g., especially sturgeon-like reconstructions; Traquair, 1887: fig. 5), care must be taken to not extend this to biomechanical inferences. Indeed, Watson (1925: 830–831) argued that the intimate connection between the jugal and maxilla of †*Chondrosteus* indicated limited mobility of the upper jaw, as is plesiomorphic for ray-finned fishes. A better understanding of overall cranial architecture in †*Chondrosteus*, perhaps through digital "re-assembly" of more intact specimens than NHMUK PV P 75108, may provide some constraints on the mandibular kinematics of early acipenseriforms. Recent investigation of feeding function in Paleozoic chondrichthyans provides a possible template for this kind work (Coates et al., 2019).

Beyond †*Chondrosteus*: Clarifying the Content of the Distal Acipenseriform Stem

The hypothesized affinities of †*Chondrosteus* have been secure since the earliest investigations of the genus in the first half of the 19th century. Although its immediate relationship to acipenserids specifically to the exclusion of polyodontids was maintained well into the 1980s (Patterson, 1982a), an association with acipenseriforms more broadly has never been seriously challenged. Perhaps more remarkably, †*Chondrosteus* still remains the most ancient undisputed member of the acipenseriform stem more than 180 years after its initial discovery. New information presented here is significant insofar as it shows that †*Chondrosteus* is *less* like extant acipenseriforms than had previously been thought, particularly in terms of anatomy of the upper jaw. Despite this new information, a broad phenotypic gap remains between acipenseriforms inclusive of †*Chondrosteus* and other actinopterygians. Several actinopterygians have, at various times, been interpreted as deeper branches of the acipenseriform lineage. Such taxa are essential to bridging the structural divide between more generalized early ray-finned fishes or "palaeonisiciforms" on one hand, and †*Chondrosteus*, which already shows profound anatomical specializations of living acipenseriforms, on the other. However, none of these candidate taxa have been as uncontroversially linked to sturgeons and paddlefishes as †*Chondrosteus*, which we maintain is the distalmost member of the acipenseriform stem that can be assigned with any confidence.

Discussion on the possible early relatives of acipenseriforms has mostly centered around a handful of fishes of latest Paleozoic and early Mesozoic age: †*Saurichthys* and †Saurichthyiformes in general; †*Birgeria*, †*Errolichthys*, and most recently †Coccolepididae and †*Eochondrosteus*. These are joined by a few Paleozoic taxa that have been more peripheral to the debate. Of this heterogeneous roster, †saurichthyiforms and †*Birgeria* represent the most persistent candidates (Schultze et al., 2021). The two have repeatedly appeared in discussions on the early evolution of acipenseriforms ever since they were independently identified as relevant to this problem by key studies published in the same year: †*Saurichthys* by Stensiö (1925) and †*Birgeria* by Watson (1925). Discussion of these and other putative relatives of acipenseriforms is dispersed across the literature, with no overarching synthesis; previous studies review some, but not all, candidates in varying detail. Our goal is to provide a high-level survey that draws together these accounts, hopefully providing a starting point for future work on the problem of the sparsely populated acipenseriform stem.

†Saurichthyiformes.— †Saurichthyiforms are a geographically widespread and anatomically specialized late Permian to Middle Jurassic group of long-bodied actinopterygians with needle-like upper and lower jaws that superficially resemble extant beloniform teleosts (Maxwell, 2016; Argyriou et al., 2018). Many later taxa show reduced squamation, but several series of large, well-developed scutes appear plesiomorphic for the group (Kogan and Romano, 2016). The link between †saurichthyiforms and acipenseriforms traces to Stensiö's (1925) pioneering study of internal cranial anatomy of several species of †*Saurichthys* from the Lower Triassic of Spitzbergen. He produced a list of ten specific neurocranial similarities between this genus and sturgeons and paddlefishes, followed by eight differences (Stensiö, 1925: 216), and a lengthy—and somewhat circumspect—consideration of other aspects of skeletal anatomy bearing on their relationships. Working with additional material from East Greenland, Stensiö (1932) reinforced his earlier ideas about the close affinity between †*Saurichthys* and acipenseriforms, placing a particular emphasis on the presence of an elongated rostrum and aspects of pelvic-fin morphology. This took on special significance as support for the derivation of both these features (and acipenseriforms themselves) within "palaeonisiciforms," contrasting with the alternative view voiced by Sewertzoff (1928) that these morphological peculiarities of sturgeons and paddlefishes were retained primitive traits reflecting their placement outside of all remaining bony fishes (see also Tsessarsky, 2022: 1364). Aldinger (1937) subsequently included †*Saurichthys* and kin among his Sturiomorpha, a group containing sturgeons, paddlefishes, and a host of other extinct taxa.

This arrangement, or one very much like it, was reiterated in several pre-cladistic treatments of †saurichthyiforms (e.g. Lehman, 1952; Gardiner, 1967). Application of cladistic approaches has yielded a range of systematic interpretations for †saurichthyiforms. Gardiner and Schaeffer (1989) argued that their "†*Saurichthys* Group" and "Chondrostean Group" (containing paddlefishes, sturgeons, †*Gyrosteus*, and †*Chondrosteus*) represented immediate sister lineages, with Gardiner et al. (2005), Xu and Gao (2011), Wu et al. (2013), and Ren and Xu (2021) likewise finding that †*Saurichthys* (or this genus plus other †saurichthyiforms) and Acipenseriformes form a clade. This view, however, is not universal. Patterson (1982a: 253) dismissed a link between †*Saurichthys* and acipenseriforms out-of-hand, a conclusion later bolstered by more detailed anatomical discussion (Rieppel, 1992) and formal computational cladistic analysis (Coates, 1999). The most recent phylogenetic studies, which incorporate greatly expanded taxon and character sampling relative to past work, do not recover a clade comprising †saurichthyiforms and acipenseriforms. Rather, they find that †*Saurichthys* and related genera are stem actinopterygians (Giles et al., 2017; Argyriou et al., 2018; Argyriou et al., 2022; Giles et al., 2023). At present, we see no reason to regard †saurichthyiforms as directly relevant to early acipenseriform evolution. However, the group remains historically significant insofar as it gave earlier workers like Stensiö a plausible model for reconciling a bony fish affinity for acipenseriforms, and for understanding reduced mineralization in sturgeons and paddlefishes as a secondary—and homoplastic—characteristic rather than a vestige of an assumed primitive gnathostome condition.

*†*Birgeria.— †*Birgeria* is a large, fusiform actinopterygian known from Lower to Upper Triassic deposits on all continents but Antarctica and Australia (Ni et al., 2019), frequently in association with †saurichthyiforms (Romano et al., 2016). It has reduced squamation, as in some †saurichthyiforms. Unlike members of that group, †*Birgeria* is snub-nosed with jaws that extend far behind the orbit and bear massive fangs. Based on the overall structure of the braincase and its reduced ossification, Watson (1925: 850) proposed †*Birgeria* as a structural intermediate between "palaeonisciforms" and acipenseriforms. Stensiö (1932) subsequently agreed that †*Birgeria* showed similarity with sturgeons, most conspicuously in reduced mineralization of the skeleton and the position of the nostril. Aldinger (1937) formalized these observations in a classification that placed †*Birgeria* not just adjacent to living sturgeons and paddlefishes, but instead as the immediate relative of polyodontids to the exclusion of acipenserids and †chondrosteids. His view was later echoed by Nielsen (1949, 1955), who regarded †*Birgeria* as "a side-branch of the true *Polyodon* stem" (Nielsen, 1949: 294). This placement for †*Birgeria* gained little traction initially, with Schaeffer (1973) and Patterson (1973) indicating that the relationships of the genus were uncertain, and Patterson (1982a) later summarily dismissing an acipenseriform affinity as he did for †*Saurichthys*. Formal systematic analyses yield conflicting results, with some finding no

link between †*Birgeria* and sturgeons and paddlefishes (Gardiner and Schaeffer, 1989; Giles et al., 2017; Argyriou et al., 2018; Argyriou et al., 2022; Giles et al., 2023), while others support a stem acipenseriform affinity for the genus, often placing it outside a clade comprising living species plus †saurichthyiforms (Gardiner et al., 1996; Xu and Gao, 2011; Wu et al., 2013; Ren and Xu, 2021). The manual solution of Bemis et al. (1997) is unique in placing †*Birgeria*, but not †saurichthyiforms (the latter following Rieppel, 1992), as related to Acipenseriformes. This led to use of †*Birgeria* as an outgroup in several subsequent analyses of acipenseriform intrarelationships (Grande and Bemis, 1996; Hilton and Forey, 2009).

*†*Errolichthys.— First described by Lehman (1952) from a single cranium from the Lower Triassic of Madagascar, †*Errolichthys* was later revisited by Nielsen (1955) based on further Madagascan material and a fragmentary example from roughly coeval strata in Greenland. Recently, the genus has been reported from the Lower Triassic of China (Dai et al., 2023). †*Errolichthys* features a bizarre combination of features, including a ventral branchial tooth plate that opposes a large dental field on the anterior half of the parasphenoid, an absent or greatly reduced maxilla, a long parasphenoid stalk, and substantial reduction of dermal ossification on the cheek and snout. Lehman (1952: 132-133) included the last two features along with several others in a list of features shared by †*Errolichthys* and †chondrosteids. Although he was impressed by the similarities between †*Errolichthys* and acipenseriforms, Lehman (1952) ultimately concluded that other features of the genus indicated that it was—like †*Saurichthys*—something of an intermediate between “palaeonsiciforms” and sturgeons and paddlefishes. Building on his earlier ideas of acipenseriform diphyly, Nielsen (1955) provided a diagram placing †*Errolichthys* and †chondrosteids as successive groups preceding acipenserids, with †*Birgeria* anticipating polyodontids. †*Errolichthys* has received virtually no attention since then. Patterson (1982a) regarded it as more acipenseriform-like than either †*Birgeria* or †*Saurichthys* but ultimately dismissed any link between †*Errolichthys* and sturgeons and paddlefishes. In reporting new material from China that is more complete than that from either Madagascar or Greenland, Dai et al. (2023) assign †*Errolichthys* to Acipenseriformes without clear justification. Many aspects of anatomy in †*Errolichthys* remain unclear, and its structure is far less understood than either †*Birgeria* or †saurichthyiforms. The genus should be a target for redescription and formal phylogenetic analysis, with mouldic material from Madagascar likely to reveal new information through μCT (pers. obs. by MF, SG). It is obvious that †*Errolichthys* is highly specialized, and its unusual branchial bite (Giles et al., 2025) seems to be a largely overlooked example supporting arguments for ecological diversification among actinopterygians during early Mesozoic (Romano et al., 2016; Cavin et al., 2024). However, we see little evidence for a close relationship between it and acipenseriforms.

†Coccolepididae.— †Coccolepidids range in age from Early Jurassic to Early Cretaceous and, apart from the oldest examples, are typically found in freshwater deposits. They are particularly noteworthy as the latest surviving actinopterygians with a “palaeonisciform” appearance. The more than a dozen species of †coccolepidids are represented by strongly compressed fossils rather than more three-dimensional material of the sort available for †saurichthyiforms and †*Birgeria*, and evidence for the coherence of the group is limited (Hilton et al., 2004: 211). López-Arbarello et al. (2002) appear to be the first to argue for a close relationship between †coccolepidids and acipenseriforms, based on an unpublished phylogenetic analysis described in a conference abstract. Subsequent examination of well-preserved material (including acid-transfer prepared specimens) of †*Coccolepis* by Hilton et al. (2004) revealed two features shared by type †coccolepidid and some acipenseriforms: pectoral-fin spines and simple, tubular scales carrying the lateral line canal along the upper lobe of the caudal fin. However, these authors only classified †coccolepidids as actinopterans rather than advocating a clade comprising Acipenseriformes and †Coccolepididae. The conservative approach taken by Hilton et al. (2004) reflects qualifications regarding these two traits. First, the fin spines of †coccolepidids are structurally distinct from those of acipenseriforms. Second, while Hilton et al. (2004) indicated the lateral line character merited further investigation, they concluded it remained too poorly established in other extinct non-neopterygians to draw any clear inferences. López-Arbarello et al. (2013) later provided the most detailed argument for the acipenseriform affinity of †coccolepidids as part of their anatomical description of the Jurassic †*Condorlepis*. They reported this genus shows several acipenseriform synapomorphies proposed by Hilton et al. (2011): median anterior process of the parasphenoid; opercle smaller than subopercle; anterodorsal process of subopercle; pectoral-fin spine; and a lateral line canal that extends along the base of the dorsal lobe of the caudal fin near the bases of the rays. They also noted several distinctive features shared with some, but not all, acipenseriforms: long, narrow supracleithrum; enlargement of the supracleithrum relative to the cleithrum; and a “Y”-shaped antorbital bone. Cooper et al. (2024) reviewed the phylogenetic placement of †coccolepidids in their description of the new marine genus †*Toarcocephalus*. They concluded that the relationships of †coccolepidids remain uncertain pending more comprehensive phylogenetic analyses sampling both acipenseriforms and “palaeonisciforms” (Cooper et al., 2024: 20), and only equivocally assigned the group to ?Chondrostei sensu Grande and Bemis (1996). This cautious interpretation appears vindicated by a recent phylogenetic analysis with broad taxonomic sampling that places †*Coccolepis* on the actinopterygian stem, remote from acipenseriforms (Stack, 2025).

*†*Eochondrosteus.— The most recent candidate advanced for a position deep on the acipenseriform stem is also the least satisfactorily known. Originally reported

as late Permian in age (Lu et al., 2005), the Early Triassic †*Eochondrosteus* is a small, fusiform fish with scales limited to the posterior caudal region (Lu et al., 2020). Available accounts provide sparse information on cranial anatomy. However, the opercle does appear to be substantially smaller than the subopercle, which bears a prominent anterior process. The jaws are short (as noted by Hilton and Forey, 2009: 428), with the maxilla lacking a strongly differentiated posterior expansion (although the exact shape of the maxilla differs between published drawings; compare Lu et al., 2005: fig. 1 and Lu et al. 2020: fig. 1). Using a modified version of the matrix presented by Hilton and Forey (2009), Lu et al. (2020) conducted a phylogenetic analysis that resolved †*Eochondrosteus* as sister to the clade comprising †*Chondrosteus*, †*Peipiaosteus*, sturgeons, and paddlefishes. However, the genus was included as part of an all-acipenseriform ingroup, thus aligning it with the clade a priori. More detailed examination of †*Eochondrosteus*, followed by incorporation in a more taxonomically inclusive phylogenetic analysis, would represent a critical test of this interpretation (Schultze et al., 2021).

Miscellaneous Paleozoic Taxa.— A series of isolated Devonian and Carboniferous "palaeonisciforms" join the core Mesozoic ensemble of reputed acipenseriform relatives. The stratigraphically oldest of these is the Late Devonian †*Tegeolepis*, which is distinguished by a pointed rostrum and weakly mineralized scales and endoskeleton. Citing these traits and others, Gardiner (1963: 300) indicated "little doubt that the Tegeolepidae were the palaeoniscoid family from which the much later Chondrosteiformes evolved". His subsequent review of early actinopterygian systematics placed †*Tegeolepis* on one of the deepest branches of the acipenseriform stem, which he populated with no fewer than nine additional "palaeonisciform" families (Gardiner, 1967: fig. 24). Subsequent studies did not support acipenseriform affinities of †*Tegeolepis* (Dunkle and Schaeffer, 1973; Schaeffer, 1973; Gardiner and Schaeffer, 1989), with more recent phylogenetic analyses placing it as a stem actinopterygian (e.g., Giles et al., 2023).

Two late Carboniferous taxa join †*Tegeolepis* as dubious Paleozoic relatives of acipenseriforms. The first is †*Coccocephalus*, an anatomically conventional "palaeonisciform" first examined in detail by Watson (1925). He considered the origin of acipenseriform fishes based mostly on evidence from †*Chondrosteus*, and did not indicate specifically how †*Coccocephalus* might relate to that group. Instead, Watson's (1925) discussion of this Carboniferous genus essentially treats it as a stand-in for primitive actinopterygian conditions. Subsequent authors seem to have taken this as indicating a meaningful connection between †*Coccocephalus* and acipenseriforms, with Aldinger (1937) and Nielsen (1949, 1955) daisy-chaining it to the group via †*Birgeria*. In her initial revision of the genus, Poplin (1974) found no particular reason to support an acipenseriform link for †*Coccocephalus*, an opinion supported by later phylogenetic analyses (Giles et al., 2023; Stack, 2025) and evidence from preserved neuroanatomy (Figueroa et al., 2023) that instead suggest it is a stem actinopterygian. †*Phanerorhynchus*, a peculiar long-snouted taxon with armor-like squamation, is the second late Carboniferous taxon sometimes superficially allied to acipenseriforms. Watson's note appended to the original description by Gill (1923) referenced the *Acipenser*-like snout but placed more weight on aspects of fin anatomy in †*Phanerorhynchus* resembling—but ultimately rated as convergent with—that of early neopterygians. Romer (1966: 56) likewise considered the similarities with sturgeons as "merely parallelism." Gardiner (1967) emphasized several similarities with †haplolepids, but his branching phyletic diagram places †*Phanerorhychus* as the immediate relative of †Saurichthyiformes plus Acipenseriformes. Bemis et al. (1997: 65) mentioned †*Phanerorhynchus* as a priority for restudy due to its possible relationship with acipenseriforms, but without suggesting specific evidence for this link. Material of †*Phanerorhynchus* is limited to an external mold of a single small individual in part and counterpart; Watson destroyed potentially informative internal molds capturing the palate and other aspects of cranial structure to better expose impressions of the cheek (Watson in Gill, 1923: 471). Given available descriptions, we see little evidence for a particularly close affinity between †*Phanerorhynchus* and acipenseriforms beyond a superficially sturgeon-like gestalt arising from a long snout and armor-like squamation. In any case, these features appear to be derived within acipenseriforms crownward of †peipiaosteids rather than more general features expected in earlier members of the group.

CONCLUSIONS AND A PROGRAM FOR POPULATING THE ACIPENSERIFORM STEM

Our tomographic study of †*Chondrosteus* supports many previous conclusions about its anatomy presented by past authors. The most significant new finding is that of separate dermopalatine ossifications along the ventral margin of the palate, obscured from the view of past researchers limited to external examination of sometimes crudely prepared material (but see Watson, 1928 for a possible exception). Presence of discrete dermopalatines in †*Chondrosteus* supports an identification of upper-jaw bones in acipenseriforms that aligns with other bony fishes, with the lateralmost bone of the upper jaw representing a maxilla (Datovo and Rizzato, 2018; Tsessarsky, 2024). Although a conventional dermopalatine series represents an unexpected plesiomorphic character for †*Chondrosteus*, this earliest definitive acipenseriform nevertheless remains highly specialized relative to primitive actinopterygian conditions (Hilton and Forey, 2009). This, combined with weak evidence for acipenseriform affinity of earlier taxa like †saurichthyiforms and †*Birgeria*, means that much of the stem of this major actinopterygian lineage remains naked. Consequently, ambiguities persist concerning the sequence of changes leading to the distinctive suite of traits characterizing extant acipenseriforms. While it is possible that fossils belonging to these deeper branches of the acipenseriform stem remain undiscovered, we suspect at least some of these taxa are already known but their affinities are, like those of most early actinopterygians (Schultze et al., 2021; Henderson et al., 2023), unclear. Morphological and molecular timescales for the divergences between major actinopterygian lineages generally place the origin of crown actinopterans in the Late Devonian or Mississippian (Near et al., 2012; Friedman, 2015; Giles et al., 2017; Hughes et al., 2018; Friedman, 2022). If correct, this implies a failure to convincingly identify any members of the acipenseriform total-group occupying the first half of the lineage's history. This problem is not unique to acipenseriforms, with a comparable gap apparent for polypterids despite interpretation of †scanilepiforms as early representatives of this lineage (Giles et al., 2017). Based on current understanding of character distribution, we anticipate that taxa on the acipenseriform stem immediately outside of the clade including †*Chondrosteus* and living species might show a range of specialized features like reduced squamation, junction of the supraorbital and infraorbital canals in the center of the dermopterotic, a slender maxilla without a substantial postorbital expansion, modest dentition, a long posterior stalk of the parasphenoid, and so on. However, based on conditions in †chondrosteids and †peipiaosteids, we anticipate these earlier stem acipenseriforms would be short snouted. Links made between various extinct fishes and acipenseriforms based on elongated rostra (e.g., †*Tegeolepis*, †*Phanerorhynchus*, †saurichthyiforms) reflects a spurious search image generated by an overreliance on living sturgeons and paddlefishes for establishing more general conditions for the clade.

In any case, a successful agenda for populating the acipenseriform stem is unlikely to be a narrowly framed research program dedicated to the recognition of early members of this lineage alone. Instead, it will require increased anatomical information on, and systematic scrutiny of, Paleozoic actinopterygians more broadly. The morphology and phylogenetic affinities of most of these taxa is not well constrained but understanding their relationships to one another and extant ray-fin lineages is a prerequisite for populating the acipenseriform stem and reconstructing the sequence of character evolution leading to today's paddlefishes and sturgeons.

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